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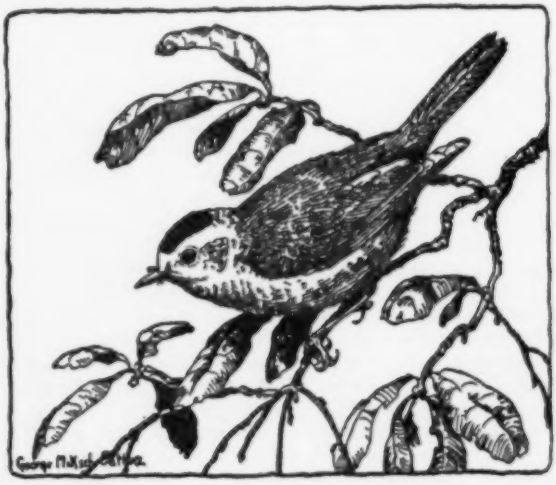

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VIOLET-HEADED HUMMINGBIRD
(Klais guimeti)

Male (left) and female (right), life-size. From a water-color by Don R. Eckelberry.

LIFE HISTORY OF THE VIOLET-HEADED HUMMINGBIRD

BY ALEXANDER F. SKUTCH

One of the smaller members of its family, the Violet-headed Hummingbird (*Klais guimeti*) is about three inches in length. On the male the forehead, forepart of the crown, chin and throat are intense violet or deep blue, according to the angle from which they are viewed. The remaining upper plumage is metallic bronze-green. The central feathers of the rounded or slightly notched tail are silvery bluish-green; the remaining rectrices are similar basally but dull black on the terminal half and narrowly tipped with light gray. The remiges are dusky purple. A white spot behind each eye gives the bird an alert, wide-awake aspect. The under plumage posterior to the throat is largely brownish-gray, spotted or flecked with green, especially on the sides. The less intensely colored female differs from the male in having the forehead and crown paler and bluish rather than deep violet and no blue or violet on the throat, her under plumage being gray, tinged with metallic green or bronze-green on the sides and flanks. In both sexes the bill, straight and of moderate length for a hummingbird, is largely black. This attractive bird was dedicated in 1843 by Mm. Bourcier and Mulsant to M. Guimet, a chemist of Lyons in France who invented a peculiar blue dye also known by his name.

Distribution and Floral Preferences

The Violet-headed Hummingbird ranges from Honduras through Costa Rica and Panamá to eastern Ecuador and Perú. In the central part of the Cordillera de la Costa of Venezuela it occurs from 200 to 850 meters (656 to 2789 feet) above sea level (Schäfer and Phelps, 1954:75). In Costa Rica, where alone I have met it, this hummingbird is found chiefly in the upper portions of the Humid Tropical Zone, between 1000 and 3000 feet above sea level (Carriker, 1910:551), on both sides of the Cordillera. Strangely enough, I did not become acquainted with it during my first year and a half in the valley of El General, where I watched birds chiefly from about 2300 feet upward. Nor did I meet it in the six months which I spent near San Isidro del General, around 2200 feet, in 1939. But the following year, working in the valley of the Rio Pacuar in the same region, I found a number of nests at about 2500 feet above sea level, and through these I became familar with the female of the species. Still, I saw no males well enough to write a description until a year later, when I found them in the valley of the Rio Reventazón on the opposite or Caribbean slope of Costa Rica. Here they were abundant around 2800 feet above sea level, along with a multitude of other hummingbirds of a number of species, and with bees, butterflies and hawk moths,

about the long rows of *Stachytarpheta*, a straggling shrub of the vervain family much used as a hedge plant in this locality.

Largely because of the attractiveness of this plant to hummingbirds, and despite its unkempt, straggling habit of growth unless kept so closely trimmed that it can scarcely flower, I planted a hedge of *Stachytarpheta* about the house which I built in 1941 in El General, by the Río Peña Blanca at about 2500 feet above sea level. When my hedge began to flower early in the following year, the Violet-headed Hummingbird was, appropriately, the first member of the family that I saw visiting its blossoms. At about the same time I discovered my first singing assemblies of the males, both near my house and at a distance of several miles.

In my experience, the Violet-headed Hummingbird is a species of peculiar distribution, fairly swarming in certain localities, yet in others nearby it is lacking, or at least so rare as to escape detection. On the one hand I associate it with deep forest, where all but two of my nests were discovered, but on the other, with *Stachytarpheta* hedges about dwellings and in pastures, often far from any forest worthy of the name. On "Silver Spring" Plantation at Murcia, on the slopes high above the roaring Río Reventazón, there were thousands of feet of these hedges planted along the fence lines and through the pastures. They were 10 or 12 feet high, so dense that cattle could scarcely pass through them, and they flowered profusely at the periods of my visits in both June and September, as they do throughout the year unless there is a severe dry season. The farm was devoted to coffee, bananas and cattle, and there was no forest in the vicinity except a few shreds of it deep in the ravines which seamed the long, steep slopes. Here *Klais* was the most numerous of the hummingbirds which gathered about the hedges in such abundance as I have rarely seen hummingbirds elsewhere, except possibly in the clearings bright with flowering shrubs and herbs on the high mountains of Guatemala, at the beginning of the dry season when blossoms are most profuse. There seemed to be one Violet-headed Hummingbird for every 15 or 20 feet of hedge. When not hovering on invisible wings before the deep purple blossoms, they rested quietly on low perches in the hedge itself or in bushes close by it. There were individuals of both sexes, mature and immature, with fully adult males in the minority. The latter were arrestingly lovely when, while hovering before the compact cluster of tiny blossoms near the middle of the long, green, whip-like flower-spike, they pointed their bills toward me and the deep metallic violet of crown and throat burst upon me in full splendor.

Companions of the Violet-headed Hummingbirds, or rather their competitors for the sweet nectar of the *Stachytarpheta* flowers, were Rieffer's Hummingbirds (*Amazilia tzacatl*) with rufous tails, Lesser Violet-ears (*Colibri cyanotus*), Brown Violet-ears (*C. delphinae*), an occasional violet and

green Wood-Nymph (*Thalurania colombica*) or brownish Longuemare's Hermit (*Phaethornis longuemareus*) that ventured out from the thickets or the neighboring wooded ravines, rarely a Green Thorn-tail (*Popelairia conversii*), and in September lovely Snow-caps (*Microchera albo-coronata*), minute creatures amazingly attired in coppery purple with snow-white caps. The Rieffer's Hummingbirds often darted at the smaller Violet-headed Hummingbirds and made them retreat.

At my own hedge, situated hard by the forest, the Violet-headed Hummingbirds had somewhat different associates, chiefly Rieffer's Hummingbirds, Snowy-breasted Hummingbirds (*Amazilia edward*) in glittering green, Lovely Hummingbirds (*A. amabilis*), Elicia's Golden-tails (*Hylocharis eliciae*), plainly clad Cuvier's Hummingbirds (*Phaeochroa cuvierii*), Wood-Nymphs, and Longuemare's Hermits. In May and June Jacobin Hummingbirds (*Florisuga mellivora*), charmingly clad in blue and white, and, from July or August until February, the surprisingly ornate mites called Adorable Coquettes (*Lophornis adorabilis*) were present. The attendance of the Violet-headed Hummingbirds varied from year to year and from season to season. In some years they became very rare in March when the drought was most intense, which is inexplicable, because if the season was not too dry the *Stachytarpheta* displayed blossoms at a time when few other plants were in flower and one might expect its nectar to be in greater demand than ever; yet in years of more extreme drought it, too, was almost bloomless at this period. Possibly the majority of the Violet-headed Hummingbirds went elsewhere in search of food, leaving only a few; but I shall later give reasons for believing that they had not gone far. By 1948, my *Stachytarpheta* hedge, after a drastic pruning made necessary by its too-exuberant growth, so languished that it was replaced by a more prosaic privet hedge, with resulting great diminution in the number of hummingbirds about my dwelling.

Voice and Courtship

As with many other hummingbirds, the male Violet-headed Hummingbirds take no interest in the nest but pass the season of reproduction by singing day after day in one particular locality, often associating in this activity with others of their kind and sex to form a singing assembly. In El General some of these persistent "songsters" among hummingbirds perform throughout the year, except for a month or two of silence at the end of the dry season when flowers are least plentiful. Rieffer's Hummingbird and Longuemare's Hermit are examples of this class. Others, including Cuvier's Hummingbird and the Band-tailed Barb-throat (*Threnetes ruckeri*), perform only in the wet season. Still others sing chiefly in the dry season; of these, Elicia's Golden-tail and the Violet-headed Hummingbird are my best examples.

From 1942, my first full year on this farm, until 1952, a singing assembly

of Violet-headed Hummingbirds was located in the tops of some tall burio (*Heliocarpus*) and other trees at the corner of the pasture a short distance from the house. Here the diminutive songsters were most difficult to see because of interfering foliage. After a decade or more of occupancy this station was abandoned, probably because the second-growth woods had become too tall and heavy; but other assemblies are still maintained in parts of the farm more distant from the dwelling. After a long period of silence, I sometimes hear *Klais* sing a little while the sun is rising brightly into a cloudless sky on a fine morning in October or November, the last months of heavy rainfall. The hummingbirds now sing in a tentative fashion, not intensely as they will do a month or two later, and on dark and gloomy mornings they are not heard at all. The volume of song increases through December, which is usually a month of sunny mornings with light or occasionally heavy afternoon showers. In January, when these showers are fewer and shorter, the birds are in fullest chorus and continue throughout the day. With sunny skies and the soil still moist after eight or nine months of almost daily soakings, the flowers are now more abundant, especially in the clearings, than at any other period of the year. But as the dry season continues and the ground becomes desiccated, plants languish and produce scarcely any blossoms. Even in years when a few light showers have relieved the drought of February, March is a month of few flowers. Now, after continuing in full chorus through most or, in wetter years, all of February, the Violet-headed Hummingbirds enter a period of silence, although a few, perhaps more favorably situated with reference to food, continue bravely to perform in March, at least in years not too severely dry.

In April, after returning rains have refreshed the earth and revived drooping vegetation, the Violet-headed Hummingbirds sing freely again. Their renewal of song corresponds approximately in time with that of Rieffer's Hummingbird, Longuemare's Hermit and Elicia's Golden-tail, which have likewise been silenced by the drought, and with the beginning of singing by Cuvier's Hummingbirds, the wet season performer which has long been mute. But whereas most of these species will continue to proclaim themselves through many wet months, with the Golden-tail and the Violet-headed Hummingbirds, the dry-season singers, the renaissance is brief. May is a month of heavy rainfall and at times one of the wettest of the entire year; before it is far advanced both of these species have entered a long period of silence.

Here in that district of El General called Quizarrá, around 2500 feet above sea level, no bird of any family so advertises its presence by voice, during the early part of the dry season in January and February, as does the Violet-headed Hummingbird. The singing males perch conspicuously—if so diminutive a creature may rightly be called conspicuous—on slender dead twigs, at heights ranging from 15 or 20 to about 60 feet above the ground. Many of

them gather to form definite singing assemblies, although some proclaim their presence at a distance from other males of their kind. The situations favored for their singing perches are: (1) at or just within the edge of primary forest, (2) the edge of a tall second-growth thicket, (3) scattered trees (preferably dead) standing in a small clearing surrounded by forest, and (4) the fringe of trees along a river flowing through cleared lands. Although the females may nest along rivulets that traverse extensive tracts of unbroken forest, and the males do at times station themselves for singing in the tops of trees well within the forest, they definitely prefer the edges of clearings to continuous heavy woodland. I was impressed with this fact on an excursion through the forest from the Río Peña Blanca to beyond the Río Calientillo early in February, 1942. Although the trees along both sides of the rough trail, to a distance of 30 or 40 feet, had been felled to permit the drying sunlight and breezes to reach and desiccate the muddy track, I heard no Violet-headed Hummingbirds except where the way led through wider clearings (then far less extensive than today) made for agriculture, yet in most of these larger openings the hummingbirds were singing.

Just beyond the Río Calientillo, in a recently-made clearing already grown up with tangled bushes and vines more than head high, I found a singing assembly unusually favorable for observation. This group consisted of at least four males in full adult plumage. Three of these hummingbirds had their stations in as many dead trees, remnants of the original forest, which formed the corners of a roughly equilateral triangle of about 50 feet on a side. They perched on exposed dead twiglets, well above the surrounding low growth, at heights of about 25, 30, and 40 to 50 feet above the ground, respectively. The fourth member of the assembly rested habitually about 40 feet above the ground in a dead tree about 100 feet distant from one apex of the triangle formed by the posts of his neighbors. At times I heard the voices of Violet-headed Hummingbirds coming from more distant parts of the clearing, but I did not succeed in seeing these birds.

Whether he sings alone or as a member of a group, each Violet-headed Hummingbird is to be found at his post hour after hour, day after day, through most of the dry season. From early morning, through the warm hours when the bright dry-season sun pours down its fervid rays from the zenith, until the cool evening shadows steal out from the long, forested ridges, the glittering little bird continues tirelessly to repeat his spirited, simple chant, interrupting it only long enough to seek food or to repel a trespasser. In their long-continued, tireless singing, as well as in the high, exposed perches they prefer, the Violet-headed Hummingbirds remind me greatly of the Violet-ears (*Colibri* spp.) as I have heard them in the highlands of Guatemala, Costa Rica and Ecuador.

The song, sharp and rapid, possesses a certain elementary rhythm. Although there is considerable variation in the utterances of different individuals, none is really musical. As he sings, the hummingbird turns his head constantly from side to side, scarcely opening his bill. Occasionally one

member of an assembly will invade the territory of a neighbor, approaching quite near his singing perch. Then the aggrieved party dashes at the offender, and the two streak away almost too fast for the human eye to follow. But that the pursuit ends without either of the participants having suffered injury is proved by the fact that within a few minutes they are back on their usual perches, chanting as blithely as ever.

The function of these singing assemblies is undoubtedly to advertise the location of the males to the females, so that the latter may come and have their eggs fertilized at the proper time. Although Pitelka (1942) concluded that North American hummingbirds maintain territories especially with reference to a food supply, and these territories may secondarily serve as mating stations, this explanation is hardly applicable to such species as Rieffer's Hummingbird, White-eared Hummingbird, *Hylocharis leucotis* (see Skutch, in Bent, 1940), Longuemare's Hermit (Skutch, 1951) and other tropical species that I have studied. That in the Violet-headed Hummingbird, as in many others, the territory proclaimed with such untiring song is largely or wholly a mating station is attested by the following facts: (1) The males sing in assemblies at the season when the females nest, and through much of the remainder of the year they are silent. (2) These assemblies are not always near the richest supply of food. Although for six or seven years the *Stachytarpheta* hedge about my house attracted many Violet-headed Hummingbirds as a source of nectar, not one established a singing perch near the hedge. The nearest assembly, about 100 yards distant in the tops of the second-growth trees between the corner of the pasture and the forest—a locality poor in flowers—remained through all these years where it was when the hedge opened its first blossoms. If the hummingbirds sang to proclaim possession of feeding territories, one would expect them to sing at seasons when there are no nests, to station themselves in the midst of the richest available stands of flowering plants, and to disperse more uniformly instead of congregating in assemblies, so that each individual could enjoy his feeding ground with a minimum of interference by others of his kind. These expectations are all contrary to the observed facts.

Notwithstanding my conviction that these singing assemblies serve to facilitate the union of the sexes, neither in this nor any other of the hummingbirds whose assemblies I have watched have I learned just what happens when a female arrives. In the first place, in these hummingbirds the sexes can be distinguished when at rest only in favorable optical conditions, and when in flight not at all. The arrival of any other hummingbird on or near the perch of a singing male invariably sooner or later leads to a pursuit, and these chases nearly always carry the birds out of sight. Wagner (1954), however, described the elaborate aërial dances of which the male and female of a number of Mexican hummingbirds engage, after the female has been

attracted to the vicinity of the singing male. Yet apparently even he scarcely ever witnessed the consummation of these courtship rites.

Just as many birds sing more or less outside their breeding seasons, some even carolling not a little when flocking in their winter homes thousands of miles from the land where they nest, so the Violet-headed Hummingbirds may repeat their tuneless verses during the wet months when I have found no evidence of reproduction. At this time they do not station themselves on high perches, nor gather in assemblies, nor continue tirelessly through the day as though life depended upon their unremitting vocal efforts. On the contrary, they choose a humble perch near the flowers that attract them and perform now and then at their leisure, when feeling well fed and happy. I have noticed this sort of singing in my garden in the wet season—but not in the dry— and I observed it particularly at "Silver Spring" Plantation in the Reventazón Valley. Here in June the male Violet-headed Hummingbirds sang a good deal, especially in the early morning, usually from low perches in or near the *Stachytarpheta* hedges, such as they chose for resting between visits to the flowers. They were not collected into definite singing assemblies; indeed, the concentration of these hummingbirds was such that the whole mountainside might be regarded as one great assembly of both sexes. In September the hummingbirds were less vocal, and in neither month did I find a nest.

The Nest

In the valley of El General, the female Violet-headed Hummingbirds begin to build their nests in the dry month of February, if not earlier, and the latest nestlings of which I have a record took flight in mid-May. The nests are built in the forest, usually above a stream, or at times above a well-shaded mountain torrent flowing between pastures or second-growth woods a short distance from the forest. The 11 nests that I have seen varied in height from 3 feet 3 inches above a narrow forest stream to 15 feet above the ground in the forest a good distance from any watercourse. Eight of these nests were discovered between March 6 and 13, 1940, along the Río San Antonio (a tributary of the Río Pacuar, which is one of the headwaters of the Río Grande de Térraba) and a narrow affluent of the first which we came to call *La Quebrada de los Gorriones*—The Hummingbirds' Brook—from the number of hummingbirds' nests, all of this species, that we found along its course.

I was at that time engaged in botanical collecting for the Museo Nacional de Costa Rica, and these sparkling mountain streams, flowing in pristine loveliness through a great tract of unspoiled rain-forest, traversed my favorite and most productive collecting ground. Day after day I pushed farther upward along their rocky beds, proceeding slowly because of the difficulty of walking along the wild fluvial pathway, and because of the number of things

to be observed, collected and enjoyed. Each bend in the stream opened a fresh prospect of enchanting beauty: a pool of fluid crystal mirroring the wide-spreading crowns of stately tree-ferns; water slipping smoothly down a long incline of rock; a cliff overgrown with the richest profusion of ferns, aroids, bromeliads and orchids; or a long, straight reach bordered by the tall and slender trunks of noble forest trees whose boughs interlocked far overhead. Among the verdure along the shores were many plants new to me and some hitherto unnamed by botanists; here I first made the acquaintance of some notable birds, and saw novel aspects of others already known to me. Here, too, I first became familiar with the Violet-headed Hummingbird; and of all the discoveries that I made along these unforgettable streams, this was the most noteworthy.

The eight occupied nests of the Violet-headed Hummingbird were found incidentally by the lad who carried my plant press and myself, without making a particular search for them, for we were busy gathering botanical specimens. They were situated along about two and a half miles of the combined courses of the Río San Antonio and its affluent "The Hummingbirds' Brook," as nearly as I could estimate distances along so uneven a pathway. In addition to the eight nests with eggs or nestlings, we noticed about an equal number that were empty, some bearing signs that the young had flown from them, thus providing evidence that the nests which already held feathered nestlings, hatched from eggs laid at the beginning of February, were not the earliest. Probably nesting had begun in January, if not in December. A nest with young ready to fly was only four feet from one in which the female was incubating two eggs. Another nest with feathered nestlings was about 40 feet from a different nest with two eggs. This was a truly remarkable concentration of hummingbirds' nests. Occupied nests as close together as even the farther separated of these two pairs are exceedingly rare, and I have on only one other occasion found two nests of any species in comparable propinquity. In the forested parts of the tropics, the nests of most kinds of hummingbirds are extremely difficult to find; and I rarely see more than two or three of any one kind in a year, even of the species most abundant in the vicinity.

These nests along the forest streams were all situated on branches projecting over the water, usually on pendulous branchlets, at heights of from 39 inches to about 12 feet above the current. Of my three nests found in other localities, one was attached to a pendent branch of a vine growing over a sotacaballo (*Pithecolobium*) tree which leaned far out over the wider Río Peña Blanca; it was situated in an inaccessible position about 10 feet above the water and 20 feet out from the shore. The river was here about 50 feet broad, flowing impetuously over a channel strewn with great boulders.

Another nest, of which I watched the construction, was also attached to a vine of the same species that hung above the same river, in this instance about seven feet above the water and well out from the shore. The single nest found at a distance from a waterway was attached to a spray of the climbing fern *Salpichlaena volubilis* that dangled beneath a palm frond in the midst of the forest, at a height of 15 feet above the ground. These hummingbirds showed a definite preference for hanging sprays as supports for their nests.

The lower of the two nests above the Río Peña Blanca was discovered in front of my house early in the morning of February 18, 1946, when so recently begun that it was still only a small tuft of moss and spiders' silk, about an inch in diameter. It was most attractively situated among the glossy foliage of the dangling vine, an epiphyte of the heath family, one of whose short petioles helped to support it above the sparkling current of the broad, rocky stream, low and murmurous at this season. The hummingbird continued her building while I sat on a boulder in the channel only four yards away; but to disturb her less I thought it preferable to watch from a greater distance and took my post on a mossy rock by the shore. It was 7:18 when I settled down and began to keep count of her visits to the nest. She brought 10 billfuls of material, mostly cobweb and a little moss, in quick succession, then two more billfuls at longer intervals, then she stayed away for many minutes. Soon after 8:00 she returned and brought 12 billfuls as quickly as she could gather them, then went away. Between 8:18 and 9:18 she came with material only three times more, whereas in the preceding hour she made 24 visits to the nest. She had brief periods of concentrated activity in building, separated by long intervals of neglect, during which she might make a few sporadic visits to her nest.

The following morning I watched again from 6:50 to 7:40 and from 8:12 to 9:50, keeping count of the number of times the hummingbird brought material to her nest in five-minute intervals. The number varied from 0 to 7, with an average of 1.4. There was one period of 43 minutes (8:12 to 8:55) when she did not visit the nest. From 6:50 to 7:40 she brought material 25 times; from 8:12 to 9:50 she came 17 times. In the entire 2.5 hours she brought material 42 times. Now, in addition to moss and cobweb, the hummingbird came with silky seed plumes for the lining. On both mornings she worked in silence and no male of her kind ever appeared. On the morning of February 21 she was still bringing material, but her structure appeared to be almost completed. By the following morning it had not changed in appearance, whence I concluded that it was finished—as much as a hummingbird's nest can ever be said to be finished, before her eggs hatch. It had been built in four or five working days. No egg had appeared in it by March 3, and by March 11 it had vanished.

The completed nest of the Violet-headed Hummingbird is a tiny, thick-walled cup, composed largely of green moss, and lined with seed down that is usually buff in color. One nest was exceptionally high and appeared to have been built on top of another of the same kind. All the nests that I have seen were beyond hearing (with my ears) of the males singing in their assemblies, but at least three of them were only a short flight away from an assembly.

The Eggs

In one nest the eggs were laid with an interval of two days, the second of them before 7:30 a.m. Each of ten nests contained two eggs or nestlings. The minute eggs are white in color and ellipsoidal in shape.

In 10 nests in the valley of El General, about 2500 feet above sea level, eggs were laid as follows: in February, 5; March, 4; April, 1.

Incubation

I studied incubation at the nest so attractively situated on a spray of the climbing fern *Salpichlaena volubilis* that dangled below the frond of a small palm tree up which it had twined. This nest in the midst of the forest was the only one of the 11 which I have seen that was not above running water. But it was not beyond hearing of the Peña Blanca River, whose roar was carried to me over a distance of several hundred yards when the wind blew from that quarter. The second egg in this nest had been laid on February 26, 1944; hence, incubation had been in progress for 10 days when I began my vigil at noon on March 7. I watched until, at 5:35 p.m., the light in the forest became so dim that I could no longer distinguish the hummingbird in her nest; then I returned at the following dawn and continued to keep watch until 11:39 a.m.

For so small a bird, the Violet-headed Hummingbird sat for surprisingly long periods. The 11 sessions that I timed ranged from 15 to 77 minutes and averaged 40.6 minutes. The 12 recesses ranged from 6 to 28 minutes and averaged 15.2 minutes. She spent 72.8 per cent of the day on her nest. Her steady sitting, as compared with some other hummingbirds that I have studied (the White-eared Hummingbird, for example) was due in large measure to the fact that she devoted very little time to seeking additional materials for her nest, never, apparently, leaving her eggs for that particular purpose. During my entire watch she brought only three or four bits of material. The three contributions that I clearly saw in her bill were brought to the nest as she returned to resume incubation at 7:18, 7:39 and 8:19 a.m.—just the period of the morning when the other female built most actively. Her shortest sessions on the eggs were in the early morning, before nine o'clock, her longest in the late morning and the afternoon.

When leaving the nest, she rose on wing directly from her eggs, not first hopping upon the rim as heavier birds do. Sometimes, after rising a short distance above the nest, she darted back and forth and up and down in a most erratic fashion, going only a few inches, or at most a foot or so, before she abruptly changed her direction, and she continued this for several seconds before she flew out of sight. At times she would return with the same irregularly oscillatory flight. Could she be catching small insects invisible to me? I heard no sound from her except the humming of her wings. She did not once alight on the nest's rim to turn her eggs; if she adjusted them at all, it must have been done with her feet. No male of her kind appeared. Soon after her eggs were laid those in the assembly nearest to her suspended singing, as they usually do toward the end of the dry season.

Growing close around the nest were a number of bushes of *Cephaelis elata*, a rubiaceous shrub whose small white flowers are borne in dense heads surrounded by conspicuous red bracts. A male Wood-Nymph made periodic visits to these flowers through the morning. The incubating Violet-headed Hummingbird never attempted to drive him away. She was equally indifferent to a little Longuemare's Hermit and to a big Long-tailed Hermit (*Phaethornis superciliosus*) which made less frequent visits to the immediate neighborhood of her nest, appearing never to take the slightest notice of them.

From this, the only nest for which I knew the date of laying, one egg disappeared on March 13, 16 days after the set was completed. The nest was then abandoned.

The Nestlings

The two occupied nests situated only four feet apart in the same bush that overhung "The Hummingbirds' Brook" were the farthest upstream of all that we found in 1940. Two hummingbirds' nests so close together formed a discovery so unprecedented in my experience that it called for further observations. A well-feathered nestling had flown from one of these nests as we approached, but I was able to catch it and return it beside its nestmate, where, unexpectedly, it was cooperative enough to remain. The day was already far spent when we made this exciting discovery; and we were obliged, after watching only long enough to convince ourselves that the neighboring nest with eggs was also attended, to hurry downward ere the dense blackness of night caught us so deep in the forest and made movement along the rocky streambed too dangerous to be contemplated. But next morning I retraced my course over the long, rough way and learned more about the relations between these two hummingbirds which were such surprisingly close neighbors.

At other nests along this stream I had already found that if I sat quietly on a rock, at no great distance and without concealment, the female would soon return to attend her eggs or nestlings. So I settled myself on a rounded stone which commanded a good view of the two nests in the same bush. The well-feathered nestlings were bright, alert youngsters which frequently preened their green plumage and from time to time beat their wings into a haze while they clung to the bottom of the nest. When an adult of their kind came within sight, they seemed to be aware of her approach at once and were all attention, uttering clear droplets of sound in anticipation of food. Apparently they were not able to distinguish their mother from her neighbor, for they called in the same fashion at the approach of either. The incubating hummingbird, as far as I saw, paid no attention to the other's offspring. But she was somewhat afraid of her neighbor, the mother of the nestlings. When the latter approached, the other, if sitting, would dart from her eggs. Or sometimes

she would continue to incubate while the mother fed the nestlings liberally by regurgitation, only to fly away as the other departed. Yet the hummingbird with nestlings was not aggressive toward her neighbor with eggs.

As at the nest in the climbing fern that I watched some years later, on approaching their nests each of these hummingbirds would alternately dart and hover, shooting for a short distance now to this side and now to that, irregularly back and forth, and at the end of each abrupt shift in position it would hang momentarily upon wings beating too swiftly to be seen. The short, abrupt, erratic darts, the sharp and sudden changes in direction, reminded me strongly of the behavior of a Jacobin Hummingbird when catching gnats above a river, or of a hoverfly. Possibly these hummingbirds were indeed snatching a few last-minute morsels from the air—I could not make sure. After darting from one side of the nest to the other for a brief period, the hummingbird would suddenly plop down into it, or alight on the rim to feed the nestlings.

These two hummingbirds, like others of their kind whose nests I had watched downstream, sometimes came to hover close above me before going to their nests; or else, after feeding the nestlings, before darting away they approached to have a nearer view of the strange monster that was spying on them. At one of the downstream nests the mother, apparently without seeing me, arrived suddenly and alighted on the rim to feed her youngsters. Then, my abrupt movement in raising my field glasses attracting her attention, she immediately left the nest and came to hover close before me. Satisfied by this examination that I was not dangerous, she promptly returned to give the nestlings what she had brought for them. This and other examinations to which I have been subjected by hummingbirds of a number of species appeared to be deliberate and purposeful acts, prompted in some instances by simple curiosity and in others by concern for the safety of their nests and offspring. They suggest that hummingbirds may be somewhat nearsighted, which is not surprising when one considers the minute size of the nests they build and of the insects they pluck from the vegetation or catch in the air.

I continued to watch the two neighboring nests with that uncomfortable feeling I sometimes have in the woods of being myself watched by unseen eyes. Of a sudden, a long, black snake mottled with yellow slid down an oblique ledge on the fern-shaded streamside cliff rising to my right. It moved rapidly without a pause until it came to rest on a rock in midstream, almost beneath the two nestlings. There it lay motionless with its foreparts raised high, to all appearances gazing up at the young hummingbirds, and, without much doubt, trying to discover by what route they might be reached. Knowing from repeated past experiences the great fondness of the mica (*Spilotes pullatus*) for nestlings, I killed it.

My only comparable example of occupied hummingbirds' nests close together is that of two nests of Longuemare's Hermit (*Phaethornis longuemareus*) which in 1955 I found only 12 feet apart, attached beneath leaf-tips of low, spiny palms in the undergrowth of the forest. In many hours of watching while the two females incubated and attended nestlings, I never saw one pay the slightest attention to her close neighbor. Each acted as though the other did not exist. These observations accord ill with the rather widespread belief that hummingbirds are highly pugnacious and intolerant of each other. Perhaps many of the dashing pursuits that one witnesses among members of this family should be ascribed to playfulness, as I suggested long ago (1940), and as Wagner (1954) believes from his observations in México to be true.

On the morning of May 17, 1942, I had the good fortune to witness the spontaneous departure of the fledgings from the higher of the nests of the Violet-headed Hummingbird that were attached to vines dangling above the rushing current of the Río Peña Blanca. When I arrived at half-past ten they were restless, preening and moving about in their narrow nest, and sometimes beating their wings into a haze while clinging with their feet to its rim. The big white spot behind each shiny black eye made the youngsters appear keen-sighted and alert. After a while an Oleaginous Pipromorpha (*Pipromorpha oleaginea*), whose snug mossy nest hung from a slender dangling root on the opposite shore, flew into the vine that supported the hummingbirds' nest. Although the little olive-green flycatcher would not have harmed the young hummingbirds, her close approach alarmed them; and one suddenly rose from the nest and flew with ease, directing its course toward the boughs above the opposite shore, where I lost sight of it.

The other youngster, instead of fleeing when the pipromorpha came by, crouched down in the bottom of the nest, where for a few minutes it rested quietly. But soon becoming restless again, it preened, then stood on the nest's rim, and clinging tightly with its toes, vibrated its wings into a haze and rose up as though it would break away from its downy anchorage. Then it settled back into the nest once more. When a large black wasp flitted among the foliage close beside it, the nestling opened its bill as though to defend itself, and when the insect hovered nearer, it flapped its wings, ready to dart away if prudence demanded a retreat. Presently the mother hummingbird came to feed this nestling that remained at home, giving no indication that she noticed the departure of the other. After a few minutes she returned and fed this same youngster once more, with nectar sipped from the long, slender flower-tubes, coral-red tipped with white, of the climbing heath in which her nest was placed.

Then about half an hour after the departure of its nestmate, the second young hummingbird spontaneously rose from the nest and soared up to alight on a slender branch of the vine about a foot higher. After a brief rest here, it beat its wings again and slowly rose another foot into the air, to a twig less than a yard above the nest. Here it rested and preened for a while. Then it flew upward yet again, until it passed from sight amid the close-set boughs of the sotacaballo tree in whose shade it was reared.

The mossy nest had maintained its shape well during the month of drenching rains to which it had been exposed. It did not burst asunder, as nests of Rieffer's Hummingbirds not infrequently do in similar circumstances. A premature fall from the nest would have deposited the young Violet-headed

Hummingbirds in rushing waters from which escape would have been difficult. These fledglings, and all others that I have seen, closely resembled the adult female in plumage.

Summary

In Costa Rica the Violet-headed Hummingbird resides in the higher parts of the Humid Tropical Zone, chiefly from 1000 to 3000 feet above sea level. It is found both in heavy forest and in clearings, where it is especially attracted to flowers of the verbenaceous shrub *Stachytarpheta*. The distribution of this hummingbird is irregular; it abounds in certain districts, whereas in others a few miles away and still within its altitudinal range it is rare or absent.

The males gather in assemblies to sing, each on his favorite perch, which is usually a slender, exposed twig from 15 to 60 feet above the ground. The assemblies are situated at or near the margin of forest or tall second-growth, in a forest-rimmed clearing with scattered trees, or in the fringe of trees along a river flowing through cleared lands. The several members of an assembly choose posts about 50 to 100 feet apart.

The male's song is sharp and rapid but lacking in melody. Singing may begin sporadically on sunny mornings at the height of the wet season in October. Gradually increasing in amount, it reaches its peak in the sunny month of January, when the hummingbirds perform tirelessly throughout the day. As the ground dries and flowers become fewer, song wanes, until little is heard in late February and March. In April, when vegetation is again flourishing, there is a renaissance of song which lasts into May.

Singing is most profuse just before and while the females are nesting, whereas it is in abeyance through most of the long non-breeding season. The song-perches are often situated where there are few flowers, while they are absent from neighboring areas with abundant blossoms. Hence the males appear to sing to attract the females rather than to advertise possession of a feeding territory.

In El General nesting occurs from January (or possibly late December) until May, but nests with eggs are most abundant in the dry month of February. Of 11 nests, 10 were above streams, at heights of 39 inches to 12 feet above the current, and one was 15 feet above the ground in the forest at a distance from water. Most were attached to hanging vines or pendulous branchlets. Eight of these nests were found in a single week along about 2.5 miles of a narrow forest stream and its tributary. Here two occupied nests were 40 feet apart and another two were only four feet apart. The owners of these nests paid little attention to each other. No male was seen in the vicinity of any of the nests.

One female built most actively between 7:00 and 8:00 a.m. In one period

of 50 minutes she brought material 25 times, and once she came seven times in five minutes. The nest was built in four or five days. The nest is a tiny, thick-walled cup, composed largely of green moss and softly lined with light-colored seed down.

The set regularly consists of two, elongated, white eggs, which in one instance were laid two days apart.

One female, watched during the daylight hours from noon to noon, took 11 sessions that averaged 40.6 minutes, 12 recesses that averaged 15.2 minutes, and kept her eggs covered 72.8 per cent of the period of diurnal activity. She brought material to the nest only three or four times, all in the early morning.

One fledgling left the nest as a small, harmless flycatcher flitted past, and the other departed spontaneously, in the absence of its parent, half an hour later.

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El Quizzará, San Isidro del General, Costa Rica, November 12, 1956

THE ORIENTATION OF DISPLACED WATERFOWL IN MIGRATION

BY FRANK C. BELLROSE

FIELD experiments designed to test the ability of birds to navigate over unfamiliar territory may be placed in either of two principal categories: (1) those in which homing pigeons (*Columba livia*) or wild birds are released at varying distances from their home loft or nest site to evaluate their ability to orient toward home, and (2) those in which wild birds are artificially displaced in their migration by space, time, or both.

This paper reports on studies made experimentally with waterfowl, the objective of which was to ascertain the ability of the birds to orient themselves when displaced artificially in some manner. To this end, three different groups of experiments were made, namely: (1) the delay of southbound juvenal Blue-winged Teal (*Anas discors*) in central Illinois until all individuals of the species had left the state; (2) the transplantation of adult and juvenal Mallards (*Anas platyrhynchos*) from central Illinois to Utah; and (3) the release of hand-reared Wood Ducks (*Aix sponsa*), some of which were transplanted from Illinois to Indiana and Wisconsin.

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O. D. McKeever, formerly of the Indiana Department of Conservation, was instrumental in determining the homing results of Wood Ducks raised in Illinois and released in Indiana. Dr. Robert McCabe, of the University of Wisconsin, determined the homing of Wood Ducks released at Madison, Wisconsin.

This paper has been reviewed and edited by Dr. Thomas G. Scott and the editorial board of the Section of Wildlife Research of the Illinois Natural History Survey.

PREVIOUS INVESTIGATIONS

Most of the investigations involving the transplanting of birds by time, place, or both have been conducted in Europe. A review of the more pertinent experiments on this problem is presented as an aid in evaluating the data of the present study.

On the Baltic sea coast at Rossitten in East Prussia, Schuz (1934) released 73 young storks (*Ciconia ciconia*) which had been detained until the middle of September, one to two weeks after the last of the local storks had left. Most of the young storks followed the normal migration route for the species, that is, southeastward toward the Black Sea. However, some flew slightly farther west than normal, as determined from recoveries in Greece and Crete; in addition, the flight of three individuals was quite aberrant, for they migrated southwestward through the Alps into Italy.

Additional experiments were made by Schuz (1949) in which young storks from East Prussia were released in western Germany, at Essen and Frankfurt, after the departure of the local storks. Although storks native to western Germany migrate southwestward, those released at Frankfurt flew southward to the Alps, and those released at Essen flew southeastward through the Alps into northern Italy. The direction taken by the transplanted storks bore a greater similarity to that followed by their parents than to that followed by the storks indigenous to the release area.

Ruppel and Schuz (1949) transplanted young and old Hooded Crows (*Corvus corone cornix*) from Rossitten to Frankfurt, Germany, in April, late enough so that the few individuals which infrequently winter there had already departed northward. Most of the released birds moved northeastward, but a number of individuals flew in other directions. Inasmuch as the Hooded Crow's normal migration route is to the northeast, most of the birds flew in the accustomed direction without the benefit of local birds to guide them.

Perdeck (1953) captured about 5,500 young and adult Starlings (*Sturnus vulgaris*) in fall migration at Texel, Netherlands, and transported them to three release points in Switzerland. Subsequent band recoveries indicated that young Starlings continued to migrate southwestwardly similar to the original direction of flight. However, the old birds were prone to fly northwestwardly to their normal winter quarters.

In North America, Rowan (1946) conducted a study of delayed migration in young Common Crows (*Corvus brachyrhynchos*). In early November of 1940, he released 54 young birds at Tolfield, Alberta, after all indigenous crows had departed. Of the 31 individuals reported, all but two were in the general direction of their wintering quarters.

McIlhenny (1934:331) shipped 276 ducks of unspecified species from Avery Island, Louisiana, to various points on the Pacific Coast where they were released. Of the 49 band recoveries eventually received, 40 were from the Mississippi Flyway, and 9 from the Pacific Flyway. He also sent 164 banded ducks to the Atlantic Coast, from which a total of 41 recoveries was received. Two recoveries were from the Atlantic Flyway, the other 39 from the Mississippi Flyway. Unfortunately, McIlhenny made no distinction between band recoveries of the same season and subsequent ones.

Williams and Kalmbach (1943:169) reported that 213 ducklings were shipped from Delta, Manitoba; Lower Souris National Wildlife Refuge, North Dakota; and Malheur National Wildlife Refuge, Oregon, to areas outside of their native flyways. Of the eight band recoveries received, only one was not from the flyway where released. However, six of the recoveries were for the same year as released, and only two recoveries were from the subsequent year.

Methods

Detention Experiments.—Blue-winged Teal for the detention experiments were obtained by bait-trapping in Mason County, Illinois, during August and September, 1952 through 1955. These ducks were then in migration from their breeding grounds in the northern plains of the United States and the prairie provinces of Canada to their wintering grounds in northern South America. Adult teal were banded and released at the trap site, but juveniles were placed in pens on the Chautauqua National Wildlife Refuge, near Havana, Illinois. Juveniles were separated from adults on the basis of the characters of the cloaca and tail feathers.

The Blue-winged Teal juveniles were banded and released on lakes from 20 to 70 miles away from the trap sites (Table 1). They were not released until observations indicated that the last of the migrating teal had departed from central Illinois 10 to 40 days previously. Most of the Blue-winged Teal had left Louisiana by the time of the later releases. State-wide waterfowl censuses made in Louisiana by Richard Yancey (personal communication) of the Louisiana Wildlife and Fisheries Commission revealed that in the fall of 1953, Blue-winged Teal numbers dropped from 180,000 on September 15 to only 1,850 on November 1; 500 remained during the winter. In 1954, Yancey found that Blue-winged Teal declined from 76,000 in mid-October to 4,000 on November 1, and he found none by December 1. In 1955, Blue-winged Teal in Louisiana declined from 233,000 in mid-October to 11,000 by the first of November and none was found by the middle of that month.

Control data for comparison with experimental data were obtained from bandings of Blue-winged Teal in Mason County, Illinois, from 1949 through 1952. As is customary in banding operations, these birds were released the same day they were trapped and banded.

Transplantation Experiments.—Mallards for transplantation to Utah were trapped on the Chautauqua National Wildlife Refuge, near Havana, Illinois, in early November, 1953. On the basis of cloacal characters drakes were separated into adults and juveniles. They were placed in pens until a sufficient number was at hand for shipment. On November 13, the Mallards were placed in crates on a stake truck, and the trip west started at 4:00 p.m. The Mallards arrived at their destination, 1,150 miles to the west, in the Great Salt Lake Basin of Utah early in the morning of November 16. Only a few ducks died en route. Adult Mallard drakes, numbering 470, were released at Utah's Ogden Bay Refuge, near Hooper. Juvenal Mallard drakes, numbering 425, were released at the U. S. Fish and Wildlife Service's Bear River Migratory Bird Refuge, 25 miles north of Ogden Bay, near Brigham City.

Control data for this experiment were provided by previous Mallard bandings at the Chautauqua National Wildlife Refuge in Illinois and the Bear River Migratory Bird Refuge in Utah.

Homing Experiments.—In 1944 young Wood Ducks were artifically reared at the Survey's Havana field laboratory for transplanting to other places. The eggs were collected from Wood Duck boxes erected in Mason County, Illinois. A report on the artificial hatching and rearing of the young has been published by Hanson (1951).

Juvenal Wood Ducks were banded and transplanted, when three to six weeks old, from Havana, Illinois, to the Jasper-Pulaski Game Preserve near Medaryville, Indiana, the University of Wisconsin Arboretum near Madison, Wisconsin, and the Tribune Farm near Wheaton, Illinois. Ninety-five ducklings were taken to the Jasper-Pulaski Game Preserve on August 7, 1944, and confined for one week before release. One hundred ducklings were taken to Madison on August 4, 1944, and were released there on August

14, 18, 22 (McCabe, 1947:105). Twenty ducklings were released at the Tribune Farm on July 20, 1944.

Control material for this experiment consisted of 90 hand-reared Wood Ducks, released within a few miles of where they were raised, on Quiver Creek, Mason County, Illinois, September 8 and 16, 1953.

The results obtained from experimental releases of Blue-winged Teal, Mallards, and Wood Ducks were determined from band recoveries. Recoveries received the same season as the bandings are termed *direct;* those received in subsequent seasons are termed *indirect.* Bands recovered from control groups of ducks provided a means of evaluating experimental results.

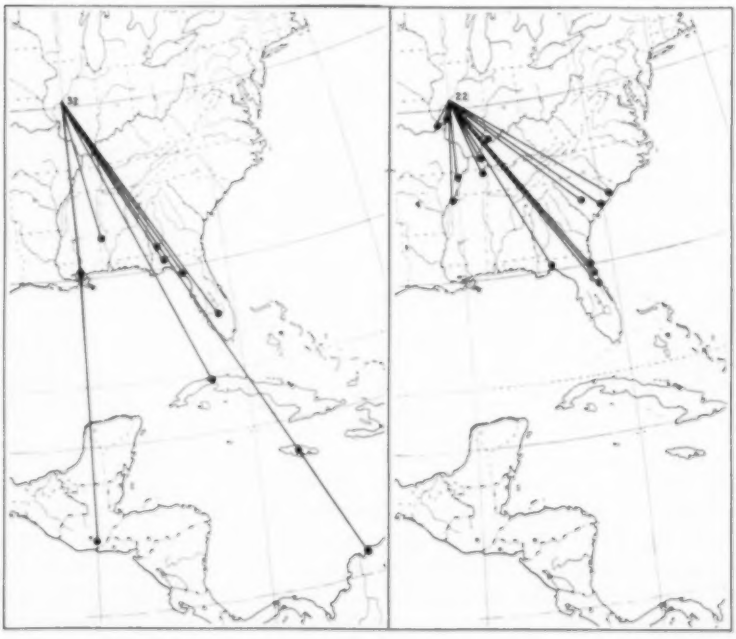

FIG. 1. *(left)* Direct band recoveries of juvenal Blue-winged Teal which were detained in fall passage until November 11, 1952.

FIG. 2. *(right)* Direct band recoveries of juvenal Blue-winged Teal which were detained in fall passage in Illinois until November 30, 1953.

EXPERIMENTS WITH DETAINED TEAL

Direct band recoveries from juvenal Blue-winged Teal detained until November 11, 1952, at Lake Chautauqua National Wildlife Refuge in Mason County, Illinois, show (Fig. 1 and Table 2) a movement to the southeast

TABLE 1

NUMBERS OF JUVENAL BLUE-WINGED TEAL RELEASED IN CENTRAL ILLINOIS AT INTERVALS AFTER THE DEPARTURE OF THE SPECIES FROM THE STATE, 1952–1955

Release Date	Lake	Number Released	Number of Direct Recoveries	Per Cent Recovered
Nov. 11, 1952	Chautauqua	393	43	10.9
Nov. 30, 1953	Chautauqua	343	38	11.1
Nov. 10, 1954	Springfield	100	11	11.0
Nov. 23, 1954	Decatur	70	6	8.6
Dec. 1, 1954	Springfield	70	6	8.6
Nov. 22, 1955	Springfield	50	4	8.0
Dec. 8, 1955	Springfield	45	3	6.7

and south. Thirty-two recoveries were made within a radius of 25 miles of the release point, and 10 recoveries were from more distant points.

In 1953, Blue-winged Teal juvenile were detained at Lake Chautauqua until November 30, when they were released there. Direct band recoveries (Fig. 2 and Table 2) indicated that there was a greater movement to the east-southeast than in the previous year. Nevertheless, six recoveries were in a southeasterly direction from the point of release, two from a southerly direction, and two from a southwesterly direction.

Juvenal Blue-winged Teal were released at Lake Springfield on November 10 and December 1, 1954, and at Lake Decatur on November 23 of that year. Recoveries later that year show (Fig. 3 and Table 2) a great deal of individual variation in movement of birds from these release points. Although one juvenile moved north 75 miles, and two flew east, and one west, most of the recoveries were to the southeast with smaller numbers from the south and southwest.

Direct recoveries from releases of juvenal teal on November 22 and December 8, 1955, at Lake Springfield show a movement to the east-southeast, southeast, and south (Fig. 4 and Table 2).

A principal reason for the spread of release dates from November 10 to December 8, was to determine if the course of migration followed by the juvenal teal changed with the sun's decreasing declination as fall progressed. Such a possibility was indicated by the greater proportion of recoveries from the east-southeast from the release made on November 30, 1953, as compared to recoveries from the release made on November 11, 1952. However, subsequent data (Table 2) indicate that there was no correlation between the course followed by juvenal teal and the sun's changing declination.

Experimental Versus Control Recoveries.—A comparison of direct recoveries from detained juvenal Blue-winged Teal (Table 2) with control data from teal banded during their normal passage through central Illinois (Fig. 5 and Table 3) is most astounding. It shows that juveniles of the Blue-winged Teal, without guidance from adults, migrated southward along routes normally used by the species, and that the proportion of recoveries along each route from experimental birds was almost identical to recoveries from control birds (Tables 2 and 3).

TABLE 2

DIRECTION OF FLIGHT TAKEN BY JUVENAL BLUE-WINGED TEAL DETAINED IN AUTUMN MIGRATION IN CENTRAL ILLINOIS, 1952–1955. (BASED UPON DIRECT BAND RECOVERIES)

Date of Release	0 to 90°	90 to 100°	100 to 110°	110 to 120°	120 to 130°	130 to 140°	140 to 150°	150 to 160°	160 to 170°	170 to 180°	180 to 190°	190 to 360°
Nov. 10, 1954							2	1	1	1	1	5
Nov. 11, 1952								7		3		
Nov. 22, 1955								1		3		
Nov. 23, 1954	2	1					2	1				
Nov. 30, 1953					2	2	4	1	1	1	1	2
Dec. 1, 1954				1				1	3			1
Dec. 8, 1955						1	1			1		
Total	2	1		1	2	3	9	12	5	9	2	8
Per Cent	3.7	1.9		1.9	3.7	5.6	16.7	22.2	9.3	16.7	3.7	14.8

The routes by which Blue-winged Teal customarily migrate from central Illinois to their winter home appear to combine in three major "trunk lines." The principal course is southeastward through Florida and Cuba to Colombia and Venezuela (Fig. 5). The next most important course appears to be almost due south to the Delta region of Louisiana, and thence across the Gulf of Mexico to Central America. A third course, apparently used by only a small proportion of teal, lies in a southwesterly direction to the coast of Texas.

Rate of Movement.—Not only did juveniles of the Blue-winged Teal exhibit individual traits as to direction of flight, but also in speed of flight. Some teal departed from the point of release almost immediately while others remained in the release area for as long as a month.

Band recoveries which indicate the fastest rate of movement by juvenal Blue-winged Teal after being detained in migration are shown in Fig. 6. Some of their speeds are indeed remarkable. One juvenile released late in the afternoon of November 10, 1954, was killed 2 days later in Florida. Two juvenal teal released in mid-afternoon of November 22, 1955, were killed together on November 24, on lower Mobile Bay, Alabama.

On the other hand, local band recoveries indicated that some of the detained juveniles stayed near the release point for 19 days in 1952 and 15 days in 1953. Field observations revealed 10 teal near the release site at Lake Chautauqua on November 28, 1952, 17 days after their release, and six were still there on December 1, but none was seen thereafter.

In 1953, Lake Chautauqua froze over on December 15, 16 days after the teal were released. For two weeks following the freeze-up, four banded teal were seen feeding along the margin of an open creek, about two miles from the release point.

The extended stay of some of the juvenal Blue-winged Teal in the area of

release would indicate either a loss in their desire to migrate or confusion as to where to migrate as a result of their prolonged detention.

Effect of Other Ducks.—It may be argued that the juvenal teal followed other species of ducks in migration. This is most unlikely. Banding data reveal that only two other species of waterfowl which frequent Illinois commonly migrate to the southeast, namely, the Pintail (*Anas acuta*) and Ring-necked Duck (*Aythya collaris*). These species were not present at Lake Springfield or Lake Decatur at the time of or immediately following the releases there. Pintails and Ring-necked Ducks were present in the Lake

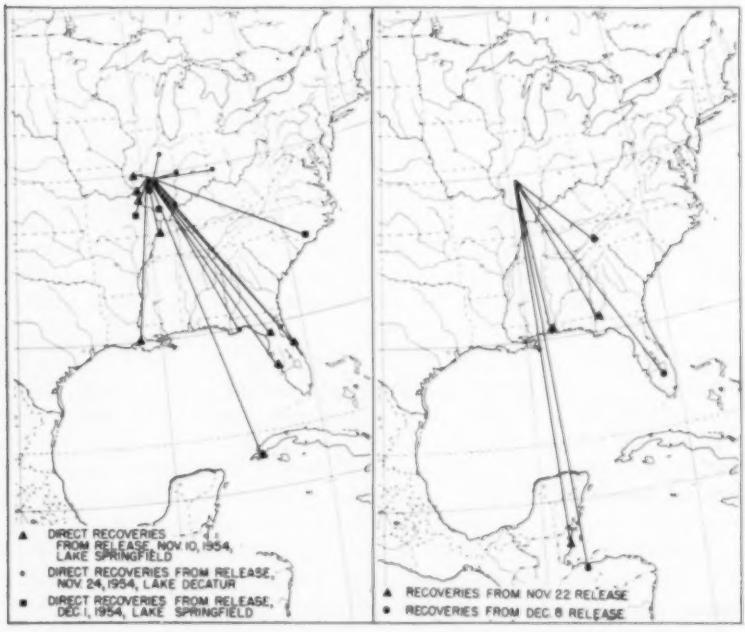
DIRECT RECOVERIES FROM RELEASE, NOV 10, 1954, LAKE SPRINGFIELD
DIRECT RECOVERIES FROM RELEASE, NOV 24, 1954, LAKE DECATUR
DIRECT RECOVERIES FROM RELEASE, DEC 1, 1954, LAKE SPRINGFIELD
RECOVERIES FROM NOV 22 RELEASE
RECOVERIES FROM DEC 8 RELEASE

FIG. 3. (*left*) Direct band recoveries of juvenal Blue-winged Teal which were detained in fall passage until November 10, 24, and December 1, 1954.

FIG. 4. (*right*) Direct band recoveries of juvenal Blue-winged Teal detained in fall passage in Illinois until November 22 and December 8, 1955.

Chautauqua area only at the time of the November 11, 1952, release. Mallards have made up the bulk of the duck populations whenever and wherever juvenal teal have been released. Thousands of band recoveries from Mallards trapped in central Illinois demonstrate that the bulk of this species migrates almost due south to Reelfoot Lake, Tennessee; Stuttgart, Arkansas; and

northern Louisiana. Fewer than 1 per cent of Illinois-trapped Mallards migrate east-southeast to South Carolina.

Furthermore, the exacting degree to which juvenal teal prorated their flight over the routes used by the species (Tables 2 and 3) makes it inconceivable that the detained teal followed other species of ducks. If they had, most of the band recoveries would have occurred between 170 and 190 degrees, rather than between 140 and 160 degrees.

Effect of Wind Direction.— It may be argued that the detained teal "drifted" in a southeasterly or southerly direction because of air mass movements. However, a study of the daily weather maps of the U.S. Weather

TABLE 3

DIRECTION OF FLIGHT TAKEN BY ADULT AND JUVENAL BLUE-WINGED TEAL BANDED WHILE IN FALL MIGRATION THROUGH MASON COUNTY, ILLINOIS, 1949–1952. (BASED UPON DIRECT BAND RECOVERIES)

Banding Period	0 to 90°	90 to 100°	100 to 110°	110 to 120°	120 to 130°	130 to 140°	140 to 150°	150 to 160°	160 to 170°	170 to 180°	180 to 190°	190 to 360°
September, 1949 through 1952	8	2				2	11	19	8	10		8
Per Cent	11.8	2.9				2.9	16.2	27.9	11.8	14.7		11.8

Bureau reveals a lack of correlation between wind direction and movements of the detained juvenal teal. To restrict the period in which weather might have influenced the direction of flight, only those movements which were charted within five days after release were considered.

In 1952, one juvenal teal was killed 700 miles to the south four days after release. The day after release, the winds between central Illinois and the Gulf of Mexico were light and northeasterly. On the following four days, the winds were light and southerly.

During the five days following the release of Blue-winged Teal on November 30, 1953, winds were light to moderate and were almost entirely from the southeast and south during this period. One juvenile flew southwestward 125 miles, one southward 275 miles, two south-southeastward 215 and 300 miles, and three flew southeastward 300, 960, and 960 miles, respectively.

From the release made on November 10, 1954, two detained teal flew 112 miles south-southwest overnight. Another teal flew 930 miles southeast in two days. Winds on November 11, were from the south at light velocities in the sector affecting the first two teal. In the region southeast of Illinois winds were from the south or east. On November 12, winds in that region were largely from the northeast.

From the release made on November 24, 1956, two teal flew east 140 and 270 miles in two days. One teal flew southeast 152 miles in four days. Winds on November 24 were 11 to 16 miles per hour from the west. On November 25 and 26, winds were still in the northwest and west from light to moderately strong.

Two teal flew south 150 miles overnight from the release made on December 1, 1954. At that time, winds were from the north at 11 to 16 miles per hour.

Two teal flew south-southeast 675 miles during a two-day period following their release

on November 23, 1955. On November 24, winds in this region were light from the northwest; on November 25, these were light from the east.

It would appear from these records that winds were adverse as often as they were favorable to a southward movement of experimental birds. Winds

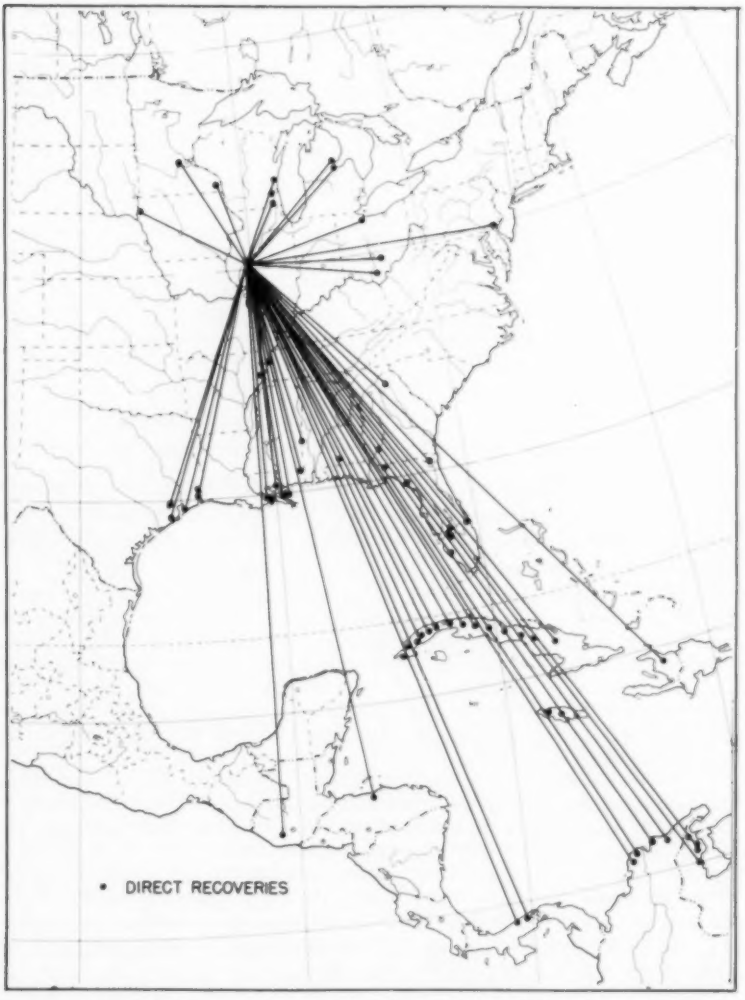

FIG. 5. Direct band recoveries from Blue-winged Teal banded during fall passage in Mason County, Illinois, September, 1949, through September, 1952.

were largely adverse for movements made after releases in 1952, 1953, and November 10, 1954. Winds were favorable for movements made following the releases of teal on November 23 and December 1, 1954. Although the direction was favorable, winds were so light following the release on Novembr 23, 1954, as to be of doubtful influence.

The only decisive movement of detained teal which might be attributed to weather is the aberrant flight of two birds to the east concurrently with moderate west winds.

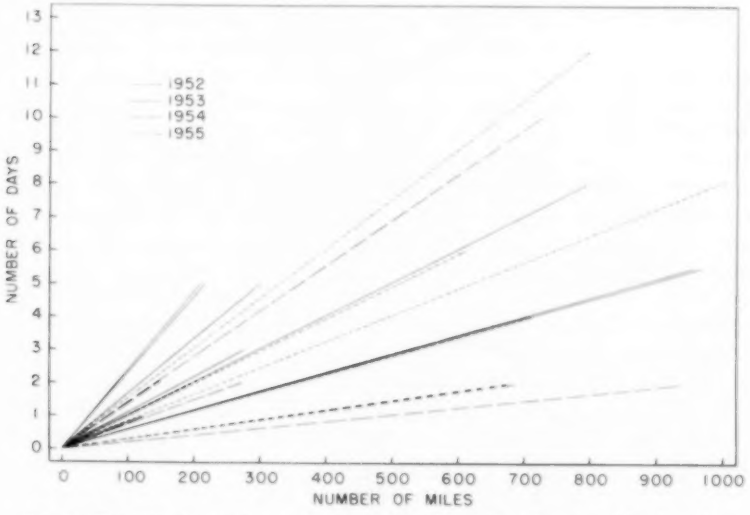

FIG. 6. The rate of migration by detained juveniles of the Blue-winged Teal as shown by band recoveries selected for their speed.

Field Observations.—Observations in the field substantiate banding data that Blue-winged Teal juveniles migrate south without adults to guide them. In trapping Blue-winged Teal during September at Delta, Manitoba, Arthur S. Hawkins of the U.S. Fish and Wildlife Service found the proportion of juveniles to be extremely high in relation to adults. In September of 1950 he trapped 133 juveniles per adult; in the same month of 1952, he caught 61 juveniles per adult. During this period, Hawkins observed Blue-winged Teal depart to the southward between sunset and darkness, usually in flocks numbering from 10 to 40 individuals. According to Hawkins, the low proportion of adults in the population at the time of departure would have made it impossible for every flock to contain even one adult. In the darkness, it would seem highly improbable that flocks remained in contact with each other.

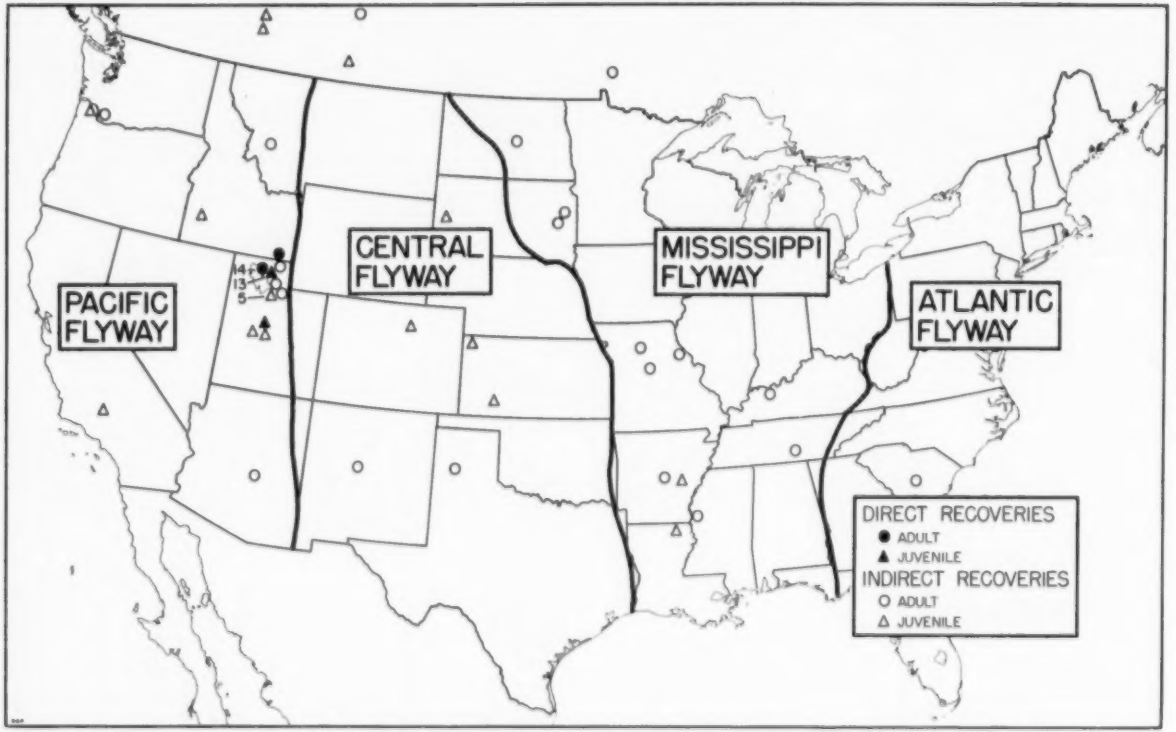

FIG. 7. Band recoveries from adult and juvenal drake Mallards trapped in Illinois and released at the Ogden Bay Refuge and the Bear River Migratory Bird Refuge, Utah, on November 16, 1953. The outline of the flyways represents a combination of both biological and political flyways to avoid the overlapping of the biological and the rigid outlines of the political.

Behavior in Pens.—The activity of captive teal also indicated a migratory incentive and an orientation response at the time the sun set. Throughout the day, during October and November, the teal dispersed through the pens, but as sunset approached they gathered in a compact group at the south end of the pens. Mallards which were held in similar pens at the same time never exhibited this behavior.

Experiments with Transplanted Mallards

Direct and indirect band recoveries from adult and juvenal Mallard drakes transplanted from Illinois and released at two different points in Utah on November 16, 1953, are shown in Fig. 7. With only two exceptions, all of the 29 direct recoveries, both adults and juveniles, were in the Great Salt Lake Basin. These three recoveries were not far outside the Basin: One adult was killed about 100 miles north; and one juvenile was taken about 150 miles south of the Bear River Migratory Bird Refuge. During the subsequent two hunting seasons, 19 recoveries of birds liberated as juveniles were recorded, and 21 of birds liberated as adults. There was a marked difference between the migration movements of adults and juveniles during the fall months of 1954 and 1955 (Fig. 7). Among adults, one recovery was in the Atlantic Flyway, 12 in the Mississippi, two in the Central, and six in the Pacific. The indirect recovery in South Carolina undoubtedly represented a bird which previously had migrated through Illinois to the Atlantic Flyway. Among recoveries of Mallards transplanted as juveniles, two were in the Mississippi Flyway, five in the Central, and 12 in the Pacific.

Band recoveries from Mallards native to the Bear River Migratory Bird Refuge, Utah (Van Den Akker and Wilson, 1949:365), show that few individuals normally migrate east of the Pacific Flyway. Van Den Akker and Wilson report that, among 145 direct recoveries, only 13 were taken outside the Pacific Flyway: two were in Colorado, one in Illinois, two in Iowa, two in Nebraska, one in New Mexico, one in Oklahoma, and four in Wyoming. Among 75 indirect recoveries, they recorded only five outside the Pacific Flyway, two from Colorado and three from Wyoming, both states adjacent to Utah.

Indirect recoveries from thousands of Mallards banded in central Illinois indicate that fewer than 4 per cent of these birds have been taken west of the Mississippi Flyway in the Central and Pacific Flyways.

It is obvious that Mallards from Illinois did not attempt to return to the Mississippi Flyway during the same season they were released in Utah. They also failed to follow the migration pattern of Mallards banded in Utah. During the first hunting season, Illinois-captured Mallards released in Utah did not migrate southward as did Utah-banded Mallards (Van Den Akker and Wilson 1949:365).

The failure of Mallards from Illinois to move far from the point of release in Utah during the first fall is attributed either to an awareness of their displacement in longitude, or to confusion resulting from the unfamiliar landscape.

If they recognized they were displaced over 1,000 miles to the west, the large displacement may have induced the Illinois Mallards to remain *in situ*. Recent studies by Matthews (1953*a*, 1953*b*, 1955) suggest that birds may have an internal chronometer that would enable them to determine longitude.

However, it is entirely possible that the transplanted Mallards were so confused by the mountains and other unfamiliar landscape features that they remained in the area of release longer than the indigenous Mallards.

The lack of direct band recoveries for the experimental Mallards south of Utah suggests that the birds wintered in the Great Salt Lake Basin or the Snake River Valley, 100 miles to the north, in Idaho, an important wintering area for Mallards in the Pacific Flyway.

From the distribution of indirect band recoveries of the experimental Mallards (Fig. 7) it is assumed that in the spring migration they moved north with Mallards of the Pacific Flyway to breeding grounds in Alberta and Saskatchewan. Although there is some intermingling of Mallards from the Mississippi, Central, and Pacific Flyways on their breeding grounds in Saskatchewan and Alberta, those from the Pacific Flyway generally breed farther west than those from the Mississippi Flyway (Aldrich, *et al.*, 1949:4). Probably few of the experimental Mallards came into contact with Mississippi Flyway Mallards on the western breeding grounds. However, on the breeding grounds, the displaced Mallards were much closer to their former haunts than they would have been anywhere else in the Pacific Flyway.

The return of about two-thirds of the adult and one-third of the juvenal experimental Mallards to the Mississippi Flyway (Fig. 7) suggests that the proximity of the breeding areas resulted in these birds' finding their way back. Because of the greater return of adult than juvenal Mallards to the Mississippi Flyway, it is believed that topographic features were used by the adults as navigation cues in returning to the Mississippi Flyway.

It can be safely assumed that adult Mallards have a greater knowledge of topographic features of the breeding grounds than yearlings. It seems reasonable to assume that displaced adults, while moving from breeding areas to molting areas, and during pre-migration flights would more likely come upon and recognize previous haunts than would the displaced juveniles.

Experiments with Wood Ducks

Recoveries and sight observations of banded hand-reared Wood Ducks are shown in Fig. 8. Direct recoveries show that most of the juveniles were killed in October and November within 25 miles of the point of release.

Because the ducklings were released near Madison, Wisconsin; Medaryville, Indiana; Wheaton and Havana, Illinois, in mid-summer, it is apparent that most of them remained near the release site until late in the fall migration period. Only two birds moved northward after release; these two, released near Havana, moved 70 miles up the Illinois River valley (Fig. 8).

FIG. 8. Recoveries and sight observations of banded hand-reared Wood Ducks released near Madison, Wisconsin; Medaryville, Indiana; and Wheaton, Illinois, in 1944, and Havana, Illinois, in 1953.

McCabe (1947:106) observed that most of the 100 transplanted ducks had left the Madison, Wisconsin, release site by November 3. However, he saw a few Wood Ducks during the winter, and the indications were that at least two hens wintered in the area. O. D. McKeever reported (letter, August 23, 1944) that 46 of the 95 released near Medaryville, Indiana, on July 14, were still at the site on August 15, and a total of 93, including some local Wood

Ducks, was counted on the entire Jasper–Pulaski Game Preserve. Several of the released ducks were live-trapped there up to October 2. As far as known, no Wood Ducks wintered that year in the Jasper–Pulaski area of Indiana.

Observations on 90 young Wood Ducks released on Quiver Creek, near Havana, Illinois, on September 8 and 16, 1953, revealed that numbers remained for over a month. Some remained on the release area through November, and two hens were shot there as late as mid-December. However, none was observed to winter in the area.

Bands recovered at a distance from the several release sites indicate that the majority of birds wintered in an area from Georgia to Texas (Fig. 8). Although this area embraces the general wintering ground for most Mississippi Flyway Wood Ducks, it represents a greater dispersal than that shown by bandings of wild-trapped birds in Illinois. One transplanted Wood Duck showed a pronouncedly aberrant flight; a hen released as a juvenile at Madison, Wisconsin, on July 19, 1944, was killed in Morris County, New Jersey, on November 4, 1944.

In the spring following the several releases of hand-reared Wood Ducks, live-trapping and an inspection of nesting sites revealed that a number of hens returned to their respective areas of release.

At the Jasper–Pulaski Game Preserve, near Medaryville, Indiana, O. D. McKeever (letter, June 9, 1945) captured a hen on April 7, 1945, and another on April 13, from the group which had been released there the previous summer. Four Wood Duck hens from this group were found later that spring in nesting houses, but one of these had been captured previously. McKeever believed that another nesting hen was banded but the bird was never captured. Therefore, five and perhaps six hens from those released the previous summer returned to breed. Drake Wood Ducks from this group were reported shot in the northern United States as follows: one on September 1, 1945, near Buffalo, Michigan, some 70 miles north of the Jasper–Pulaski Game Preserve; one on November 5, 1949, in Porter County, Indiana, 35 miles north of the release area; and one on November 15, 1948, at Clinton, Iowa, some 180 miles to the northwest (Fig. 8).

According to McCabe (1947:106–7) two hens from the ducks released at Madison, Wisconsin, in the summer of 1944 were found on nests the following spring, May 21 and 22, 1945. During that summer, three Wood Duck broods were seen in the area, and the hens with the broods were believed to be birds from the release which were in addition to the two found on the nest. Thus, probably five hens from the release group nested in the Madison area, but possibly two of these hens may have been those observed during the winter. A male from this group was shot on October 17, 1945, near Rice Lake, Wisconsin, about 200 miles to the northwest (Fig. 8). A Wood Duck hen returned the following spring to the Tribune farm near Wheaton, Illinois.

The three foregoing releases, as mentioned under Methods, represented Wood Ducks which were reared at Havana, Illinois, and transported near the flight stage to areas 175 to 200 miles away. The release of young Wood Ducks near Havana, Illinois, in September of 1953, represented birds which were reared there.

In the spring of 1954, at least three hens returned to the Havana area. Two were found in nesting houses on the area where they were released; one was found in a nesting house about four miles distant on the Chautauqua National Wildlife Refuge.

Hand-reared Wood Duck ducklings appear to remain on or near the area of release through late summer and early fall even when raised to flight stage elsewhere. Some of these birds appeared to be tardy about migrating southward as shown by those overwintering at Madison, Wisconsin, and birds which remained abnormally late on Quiver Creek, near Havana, Illinois. Brakhage (1953:476) reported that hand-reared Mallards may migrate somewhat later than wild-trapped Mallards; his data (p. 471) on Pintails and Redheads (*Aythya americana*) indicated no important differences in this respect.

Young Wood Duck hens exhibited a strong homing response to the area they inhabited during late summer and early fall preceding migration. Even though Wood Ducks were raised until 6 to 8 weeks of age at Havana, Illinois, there was no indication of their direct or indirect return to that area when transplanted 175 miles northeast to the Jasper–Pulaski Game Preserve in Indiana or 200 miles north to the University Arboretum at Madison, Wisconsin.

At the Delta Marsh in southern Manitoba, Brakhage (1953:472–473, 476) concluded that the proportion of hand-reared Mallards and Pintails which homed to their natal marsh was similar to that of wild-trapped birds banded on the same marsh.

Less is known about the movement of drakes among the Wood Ducks released as juveniles in Indiana, Wisconsin, and Illinois: Four indirect recoveries north of their respective areas of release, suggest a degree of homing, but one which is not as precise as that shown by hens released as juveniles. Less precise homing may have occurred as a result of the mating of these drakes on the wintering grounds with hens that homed to their own natal areas. Possibly they may have returned unmated, and wandered about seeking a mate.

Discussion

The longer a duck remains in an area, the greater is its homing attachment to the area. Wood Ducks raised for six to eight weeks near Havana, Illinois, had no affinity for that area when transplanted only 175 to 200 miles away. A small proportion of Mallards which were several months old when transplanted from the Mississippi Flyway, to the Pacific Flyway, returned to their

original flyway the following fall. Adult Mallards exhibited a greater propensity to return to their original flyway than did juveniles.

The relationship between the age of a duck and its affinity for a particular geographic area would appear to be related to memory of topographic features. Wood Ducks which spent the first few weeks of their lives in pens at Havana, Illinois, had a very limited knowledge of their surroundings. They certainly had no innate cue which resulted in their return to the *natal* area. In the two or more months these birds spent in new areas prior to the fall migration, they surely became well acquainted with the topography of their foster home. The knowledge of topographic features acquired locally probably enabled the "Woodies" to return with competence to their foster home in the spring. Other environmental cues may play a role in the long-distance migration of Wood Ducks, but near their summer home memory of familiar landmarks must be uppermost. Griffin (1955:180) classifies this as Type I homing which he defines as a "reliance on visual landmarks within familiar territory and the use of exploration or some form of undirected wandering when released in unfamiliar territory."

Young mallards, several months of age, had had an opportunity to become acquainted with many topographic features of the Mississippi Flyway by the time they were trapped in Illinois during their first fall migraton. Obviously, however, the topography of the breeding grounds and the Mississippi Flyway would be more firmly imprinted in the memory of the adult Mallard than in that of the juveniles. Both adult and juvenal experimental Mallards were equally exposed to the topographic features of the Pacific Flyway, and, apparently, these features become more firmly imprinted on the juvenile's than upon the adult's memory.

There can be little doubt that some birds remember visual patterns over a period of time, but the degree of visual retention appears debatable. An experiment by Skinner (1950:200–201) suggests that Common Pigeons (*Columba livia*) have an excellent retention of visual patterns. He conditioned 20 pigeons to strike a particular feature on a large translucent key upon which a complex visual pattern was projected. Groups were tested at the end of six months, one year, two years, and four years. Even after four years, the group of four tested showed immediate response. One bird struck the key within two seconds after the appearance of the visual pattern and continued to respond for the next hour. On the other hand, Matthews (1955: 56) found that six visits to a particular release point were necessary before pigeons showed good orientation solely from the use of landmarks. This suggests that it may take a considerable time for birds to learn a particular landscape feature, but, once learned, it is retained for a lengthy period. Adults, therefore, would have a greater retention of landmarks than juveniles as a result of their longer association with their haunts.

Although the above discussion points up the apparent importance of topographic features and visual memory as used by waterfowl to orient themselves, it is not intended to imply that they are the only cues used by waterfowl in migration. The ability of juvenal Blue-winged Teal to migrate southward from Illinois without the guidance of adults, and over terrain never before seen by these birds, demonstrates that other environmental cues are available for determining direction of flight.

Hochbaum (1955:209) believed that: "all young waterfowl which do not join in mass migrations are inevitably destined to travel toward the equator in autumn by the dominant flow of the air mass in which they move." As shown previously such an environmental influence was not responsible for the movement of Blue-winged Teal juveniles along routes normally used by the species.

There can be little doubt that Blue-winged Teal have an innate means of determining direction. Griffin (1955:180) calls this Type II homing which he defines as "that by which birds are able to fly in a certain direction even when crossing unfamiliar territory."

The studies by Schuz (1934, 1949), Ruppel and Schuz (1949) and Rowan (1946), discussed earlier in this paper, indicate that other species of birds also possess an ability to fly in one direction over unfamiliar terrain.

The ability of waterfowl to migrate in a given direction over unfamiliar territory may be related to the use of celestial bodies or patterns as navigation cues. Studies by Kramer in Germany (1950, 1952), Matthews in England (1953*a*, 1953*b*, 1955), Griffin and Goldsmith (1955) and von Saint-Paul (1956) in the United States demonstrate that a number of species of birds use the sun as a means of orientation. However, many waterfowl migrate at night when sun orientation would have to be by considerable indirection.

Although the use of the sun for orientation has not as yet been demonstrated for waterfowl, it seems reasonable to assume that juvenal Blue-winged Teal used the setting sun, or some celestial pattern at night, to be able to migrate southward over unfamiliar territory without guidance by adults.

Probably juvenal Wood Ducks released near Madison, Wisconsin, where there was no local population, employed both Type I and Type II homing in returning to that area the following spring. The sun, or a nocturnal celestial pattern, may well have provided the cues for southward and northward migration, and visual memory of local landmarks, the cues necessary for such a display of precise homing.

Not all individual ducks, however, may have the same inherited ability to navigate. The juvenal Wood Duck, which was released at Madison, Wisconsin, and flew 775 miles east-southeast to be killed in Morris County, New Jersey (Fig. 8), was apparently almost 90 degrees off its proper course.

The two juvenal Blue-winged Teal which flew east from Lake Springfield, Illinois (Fig. 3) may have taken the wrong celestial cue.

There was no evidence in these experiments with displaced Blue-winged Teal, Mallards, and Wood Ducks of Type III homing, described by Griffin (1955:180) as allowing "the bird possessing it to choose approximately the correct direction of its home even when carried into unfamiliar territory in a new and unaccustomed direction." The Mallards transplanted from Illinois to Utah would especially qualify for the prerequisite of "unfamiliar territory in a new and unaccustomed direction," but, as previously shown, there was no indication of a direct movement toward the Mississippi Flyway.

Summary

1. Experiments were made with Blue-winged Teal, Mallards, and Wood Ducks to ascertain their ability to orient themselves when displaced artificially in some manner. Juvenal Blue-winged Teal were delayed in autumn migration until the species had left Illinois, and, in some cases, the United States. Mallards were transplanted in November from central Illinois to central Utah, 1,150 miles to the west. Wood Ducks hand-reared to flight stage in Illinois were released in Illinois, Wisconsin, and Indiana.

2. Blue-winged Teal were trapped in Mason County, Illinois, during September, 1952 to 1955, the adults banded and immediately released, while the juveniles were placed in pens. The juveniles were banded and released on November 11, 1952; November 30, 1953; November 10 and 23, and December 1, 1954; and November 22 and December 8, 1955.

3. A comparison of recoveries from Blue-winged Teal banded during their normal fall passage through Illinois with recoveries from the detained juveniles, revealed similar directions of migration for both groups. Some of the detained juveniles migrated to the southern part of the United States within a few days after release, but others remained near the release site for two or more weeks. There is ample evidence that detained birds did not follow other ducks to reach their destination, nor were air movements responsible for their southward flight.

4. Data on flock sizes and age ratios of Blue-winged Teal at Delta, Manitoba, suggest that many flocks depart in southward migration without adults to guide them.

5. Direct recoveries of bands from 470 adult drake Mallards and 425 juvenal drakes, trapped in Illinois and released, respectively, at the Ogden Bay Refuge and the Bear River Bird Refuge in Utah in November, showed no movement toward the Mississippi Flyway. Practically all direct recoveries were in the Great Salt Lake Basin.

6. Indirect recoveries after the breeding season revealed that about two-

thirds of the adult Mallards returned to the Mississippi Flyway, whereas two-thirds of the juveniles remained in the Pacific Flyway.

7. Some Wood Ducks hand-reared at Havana, Illinois, were released locally and others were transplanted to Madison, Wisconsin, Medaryville, Indiana, and Wheaton, Illinois. All groups remained in the release area through late summer and into early autumn. Some of them were tardy in migrating southward, and a few remained over winter.

8. Young Wood Duck hens exhibited a strong homing response to the area they inhabited prior to their fall migration. There was no indication of the return of any transplanted Wood Ducks to their natal home.

9. The longer a duck remains in an area, the greater its homing attachment to the area. This suggests that increased propensity to home with increasing age is related to memory of topographic features. Homing on the basis of visual landmarks within familiar territory and exploration in unfamiliar territory has been classed by Griffin (1955:180) as Type I orientation.

10. Not all waterfowl migrate by means of Type I. Blue-winged Teal have an innate means of determining direction as shown by the southward migration of juveniles over unfamiliar territory. This has been classed by Griffin (1955:180) as Type II orientation.

11. There was no evidence in these experiments of what Griffin (1955: 180) calls Type III orientation. This has been described as the ability of a bird to choose the correct direction of its home when transplanted to unfamiliar territory and direction.

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SOME BIOLOGICAL PRINCIPLES APPLICABLE TO SONG-BEHAVIOR

BY CHARLES HARTSHORNE

ALTHOUGH the singing of birds has been carefully studied in several countries, we are far indeed from a complete scientific understanding of this phenomenon. There are accurate descriptions, which I for one could not rival, of the songs of one or two regions (Saunders, 1935, 1951); there are some penetrating reflections upon general questions, such as why birds sing at all. (Perhaps the best is still the chapter by the great exponent of the role of territory in bird behavior, Howard, 1920; but see also Craig, 1943). What has been lacking is the attempt to use general principles to explain differences among species with respect to song development. I believe that sufficient information now exists to make reasonable a tentative effort to span the gap between specific or regional studies and broad generalizations about song birds, as a group and the world over. We should, for instance, be able to understand in some degree why song is little-developed in some species or families and well-developed in others; and, even, why some species have a certain complex mode of singing and others a very different though equally complex mode. Unless general principles expressing the biological bases and functions of song do thus help to illuminate particular aspects of song-behavior, they must be regarded as insufficiently established; for science is not content with blanket explanations which fail to particularize themselves in the direction of specific cases. The following are proposed as principles of singing which have enough of the self-particularizing power spoken of to deserve further consideration. (The order in which the generalizations are listed is not one of importance; thus 9c, concerning the role of territory, is perhaps the most important of all.)

1. Class Limitation

In every class of animals, e.g., insects, batrachians, and birds, in which some skill, such as singing, occurs, there are upper limits of flexibility, complexity, or other refinements, in the possible development of this skill—limits imposed by the basic anatomy, especially neural, of the class. In ability to produce "musical," or patterned sounds, birds have in most respects high upper limits, compared to batrachians, and perhaps still higher compared to insects. Nevertheless, even birds operate musically within narrow limits. Thus, whereas a human musician can learn by heart a composition occupying 50 minutes, or 3,000 seconds, the longest fixed bird song, proved to be such, that I happen to know of is the Winter Wren's (*Troglodytes troglodytes*) song of eight or ten seconds. There may (I doubt it) be a few twice as long—that is to say, less than 1 per cent of the human case. The vast majority of birds

is limited to patterns of less than four seconds' duration. Some birds can undoubtedly learn human tunes correctly, provided they are very short. I have heard a Talking Mynah (*Gracula religiosa*), in the Brookfield Zoölogical Gardens of Chicago, sing the musical refrain of "The Farmer in the Dell" with precision, save that the last portion, corresponding to the final repetition of the title phrase, was omitted. The performance took about seven seconds. In the achievement of pure musical tones (free from enharmonic partials), birds come far closer to us. Few if any musical tones are purer than those of some birds, for example, chickadees (especially *Parus atricapillus*), White-throated Sparrows (*Zonotrichia albicollis*), Woodlarks (*Lullula arborea*), Australian Pied Butcher-birds (*Cracticus nigrogularis*), many wrens and thrushes. Harmonic intervals in successive notes, even, in a few cases, simultaneous ones, are also found (Saunders, 1935, 1951), as in the Wood Thrush (*Hylocichla mustelina*), and Swamp Sparrow (*Melospiza georgiana*). In range of pitch, too, avian capacity is respectable, for the better singers dispose of at least one-half an octave, and some about three octaves, comparable to the best human voices, though not of course to an orchestra. In variety of singing a bird is vastly more restricted than a human musician. Yet an Eastern Meadowlark (*Sturnella magna*) was heard by Saunders to sing "53 different songs in less than an hour." These songs are simple, three to six notes each, making a total repertoire of somewhat less than 300 notes. Nightingales (*Luscinia megarhyncha*), with "24 stanzas," each containing on the average perhaps 11 notes, have a similar total, which is apparently somewhat exceeded by Carolina Wrens (*Thryothorus ludovicianus*), one of which according to Borror (1956) had 22 songs, each composed of at least 20 notes. Highly imitative birds have been known to sing, in individual cases, several dozen distinct imitations, besides some nonimitative passages, and it may be that the total would approach 500 or 600 notes. Very different is an insect repertoire, if one may speak of such a thing: usually a few notes, at most 20, would encompass it. Thus a species of katydid, or tree cricket, sang several little "songs," distinguished from one another only by the diverse numbers of repetitions of one sound within rhythmically separated groups. One individual had groups of 2, 3, and 4 notes; another of 5, 6, and 7. At the opposite extreme, a human musician may have a repertoire, performable from memory, of hundreds of thousands or millions of notes. The concept of class limitation can thus, in some of its aspects, be definitely quantified.

2. Species Limitation, or Specialization

The upper limits of skill in any one species are much narrower than in those of its entire class as a whole; for, although some species are close to the class limits in certain respects, none is close in all. No bird, no matter how "gifted," can equal the feats of all the others. There is and can be no

"lark and nightingale rolled into one" (Burroughs). Such statements are not made by careful observers, of proven accuracy in this field; and I hold that they contradict biological law. Animal skill is always specialized, a matter of doing some things well by sacrificing the ability to do various other things. Even the superiority of one entire class to another is not superiority in all respects. Achievement is always in some fashion exclusive or one-sided. The least creature in nature has some power not fully shared by any other, even our glorious selves. Birds can sing at higher pitches than we, and at high pitches they sound more musical than any of our instruments; also they can sing more notes per second. And a bullfrog (*Rana catesbiana*) has a better bass voice than perhaps any bird. Nevertheless, in most respects, we far surpass birds as musicians, and they surpass batrachians, though to a lesser degree. But the gap between these three classes of animals is worlds greater than that between one species of the oscinine suborder, the song birds, and the remainder. No songster is a super-bird, able to soar above the others in *all* respects of musical capacity. Of course, some species have an essential, over-all superiority to many others (indeed, of these others some do not sing at all); but we should expect to find, and we do find, if we look widely and with care, a considerable number of species that come so close to the avian limits in several respects—though never in all!—that our choice among these superior songsters is rather an exercise of taste than a contribution to knowledge. One could compile a long list of species which have been declared the finest in the world. Many birds in this country have been preferred to the Mockingbird (*Mimus polyglottos*), even by veteran Southern observers (see, for example, Wayne, 1910:181). One somewhat eccentric British writer prefers four other British songsters to the Nightingale, and quotes a farmer who preferred a fifth! The only dogma permissible here, I suggest, is, "There is no 'finest singer'!" But if this is rejected, then with Chapman I should nominate the Slate-colored Solitaire (*Myadestes unicolor*) of Middle America, known to me through recordings by Irby Davis. But its song, too, has limitations, compared to some others. It is still only a bird singing.

One may seek to evade the principle of exclusive specialization by holding that singing itself is a specialty. Yet no bird can sing as a human being can, and no insect or batrachian as some birds can; and this is enough to show that singing as such is not a definite specialty. A *particular way* of singing must be developed, and this always means that the door has been closed to other ways. Even of human performers this is true, much more of avian. Another, more subtle, evasion is to think of imitation as a specialty. This, too, will not do; we now know that imitation is no magic instinct by which what is done by one individual is simply duplicated by another. Rather an individual imitates, more or less closely, and after considerable groping and practice (often *sotto voce*, in the case of singing) only what it is, by its own

tendencies and structure, fitted to accomplish and find interesting; and in all this there are bound to be, and there observably are, sharp limitations, exclusive specializations. A highly imitative species must be one with no very strong fondness for any one musical pattern; it must have a rather loose sense of over-all musical form. It cannot care too much whether a sound be harsh, a sprawling handful of notes, a mediocre or brief tune, or an elaborate musical structure; except—and a notable exception this!—that it will disfavor the last. For even an imitative species has to have some style, some unity of pattern, of its own; hence like all medleyists, it must utilize other compositions (of any length) only in snatches. This is true of the Mockingbird (Nice, 1931) and of the Lyrebirds, *Menura* (Hartshorne, 1953); they prefer to copy brief, often unmusical songs or mere call notes; or to take bits, torn out of their musical context, from the more elaborate and highly organized songs. To take one of a Wood Thrush's five or six exquisitely contrasting, musically related phrases, almost never repeated immediately by the thrush, to stylize and simplify this phrase, missing something or much of its musical quality, to utter it two to four times in succession, and then to bury it in a medley of loosely connected, and often not very musical stanzas, is, I submit, a far cry from duplicating the thrush's musicianship. I once asked a veteran observer of Southern birds what he thought of the Mockingbird's imitations of the thrush. "Poor" was his entire reply. To the same query regarding imitations copying the Eastern Meadowlark (I have yet to note even an attempt at this), he answered, "Not very good." In Australia (Hartshorne, 1953:116f) I spent many hours listening to the stunning performances of both species of Lyrebirds, and to the several forms they were imitating; and I never once heard what seemed to me a full duplication of any of the most musical of Australia's other species. I conclude that vague or suspiciously absolute statements by enthusiasts, though acceptable as expressions of feeling, should not convince us that the principle of exclusive specialization can be transcended. Imitative species have their own remarkable skill, entirely deserving of admiration, but it is *their* skill, not that of the other highly developed songsters around them.

3. Necessary Versatility or Monotony Avoidance (Hartshorne, 1956)

There is a general minimum of flexibility or variability in singing for an entire class, and a special minimum for a species, below which individuals will not fall. There are two aspects of such variability: (1) contrasts in the musical patterns themselves; (2) pauses (measured in seconds: beyond that the bird is merely not singing) between utterances long enough to permit other activities, such as preening, listening to rivals, hopping to another twig, feeding, perhaps just idly sitting, or watching the surroundings. The anti-monotony tendency shows itself statistically in this, that as pauses grow

shorter (or as "continuity" of singing increases), the variety of utterances almost always increases. The shortest pauses (a second or so) are thus almost exclusively found in the most versatile singers—mockingbirds, lyrebirds, skylarks, numerous thrushes and wrens; whereas the longest pauses (5–10 seconds, even when the bird is stimulated by rival or lack of mate) are characteristic of the highly repetitive singers—e.g., most American warblers (Parulidae), most emberizine finches, and a host of other forms around the world (Hartshorne, 1956:184–185). (Outside the songbirds, the domestic rooster [*Gallus gallus*] is a good example.) Even within the same species, the law is often strikingly illustrated; for there may be two styles of singing, a repetitive style with long pauses, and a versatile style (usually occurring at dawn or dusk) with short ones. The most spectacular case is that of the Eastern Wood Peewee (*Contopus virens*), which Craig (1943) has studied with infinite care. However, the Canada Warbler (*Wilsonia canadensis*) and the American Redstart (*Setophaga ruticilla*) are only a little less striking in this respect (Hartshorne, 1956:185–187). A few species have unusually low minima of variability, or (the same thing) unusually high "monotony thresholds," but these are mostly non-Oscines, a fact significant in itself: thus the Least Flycatcher (*Empidonax minimus*) or the Whip-poor-will (*Caprimulgus vociferus*); but also, it seems, Hutton's Vireo (*Vireo huttoni*) and doubtless a few (a very few) other songbirds. The general trend is overwhelming: repetitiveness and short pauses are rarely combined.

4. Maximal Continuousness

Pauses tend to be as short as (subject to the previous principle) the bird's musical versatility permits; i.e., versatile singers do not regularly employ long pauses, just as repetitive ones do not use short pauses. Thus the two principles can be combined, into

3, 4. The Positive Correlation of Continuity and Variety

Most of the famous songsters of the world illustrate high values both in variety and in continuity; most of the "poor" singers illustrate low values in both; and it is rare to find a high value in one with a low value in the other. (It should be understood that "variety" here (like "continuity") means, in the short run: change in theme, or in rendition of a theme, within a dozen seconds or less. Birds with a repertoire, but which sing each song a good many times before shifting to another, do not count as highly versatile for the purposes of this law.) Why are these two variables thus correlated? The avoidance of the combination, short pauses with repetitiveness, seems simply to show that, like all creatures, birds require change to sustain interest in an object or activity. When a pattern has been sung, there is, therefore, a temporary inhibition lasting some seconds upon singing that pattern over

again (unless perhaps a few times, and even then, only if it be very short). But this inhibition fades rapidly, in birds much sooner than in us; for birds live in shorter time spans than we. Since the inhibition against repeating the same pattern does not hold against singing a contrasted one, a bird which performs several different songs or phrases is free to sing again immediately. Why, however, does it tend to use this freedom (principle 4)? One can think of three possible answers: (1) variety would be useless if pauses were so long that the bird (performer or listener), being a short memoried creature, no longer felt the effect of the previous utterance; (2) there may be competitive advantage for maintenance of territory, or of ethological isolation, or for finding a mate, in keeping up a steady stream of sounds; (3) if a bird likes to sing—otherwise, would it develop variety?—and if there is no disadvantage, why should it not keep at it uninterruptedly, provided the inhibiting effect of repetition can be avoided? These reasons seem mutually compatible, and amply explanatory of the fact that long pauses are as rare with variety as short ones without it, and that medium pauses and medium variety go together. As a result, one may in general, and rather closely, infer the degree of continuity normal to a species from its normal versatility, or vice versa. A corollary is that highly imitative birds, which of course are versatile, tend to be continuous singers.

5. Spatial Detachment of Continuous Singing from Place of Feeding

(I owe this to a suggestion of Dr. Olin Sewall Pettingill, Jr.) Species which sing with much variety, and hence continuously, sing from perches separated from their feeding grounds; whereas many, probably most, interrupted or discontinuous singers sing and feed in about the same places. Typical continuous singers: Skylarks (*Alauda arvensis*), feeding on the ground and singing in the air; numerous members of the thrush and the mockingbird-thrasher families, feeding on the ground and singing in trees or bushes (or —*Turdus merula*—from house tops); lyrebirds, singing from a specially constructed mound on which they also "dance", and feeding elsewhere, over a wide area, on the ground. Typical interrupted singers: Old and New World warblers (Parulidae, Sylviinae), Australasian whistlers (Pachycephalinae), which mostly sing and feed in the branches; American meadowlarks (*Sturnella*), which feed and often sing on the ground; flycatchers, in both hemispheres (Tyrannidae and muscicapids), which sing on perches from which they also sally out to catch insects. Reasons for the law seem clear enough. If food is immediately accessible, it tends to distract from song; also the system of interweaving snatches of song with bits of food-getting has advantages, since it provides song sufficiently continuous for most purposes, and enables food-seeking to go on without much interruption. In treeless areas, moreover, it is the natural alternative to prolonged

flight song, which is strenuous. Also, species living *entirely* in trees have little occasion to seek a special song perch; whereas ground-feeding species in areas not lacking in trees can sing much more safely and effectively from an elevated perch, whence they cannot, without loss of efficiency, descend every few seconds for moments of feeding. Interesting special case: Eastern Wood Pewee, which as a rule sings its special, continuous song, but not its usual discontinuous one, from a special tree, and at times of day (dawn and dusk) too dimly lighted for passing insects to be readily seen (Craig, 1943:36–37).

The Red-eyed Vireo (*Vireo olivaceus*) seems something of an exception to principle 5; for it often sings rather continuously in the trees in which it also feeds. However, its phrases are all short and without much musical connectedness, and in this sense its singing lacks continuity. Some of the Old World warblers which live in swamps (genus *Acrocephalus*) seem not to fit well either. Yet the general trend seems unmistakable.

6. The Correlation between Quantity and Quality

Many species (I believe the great majority) which sing elaborately and "well", by customary standards, also devote an exceptionally large part of the day, and ultimately the year, to singing. If we take the lengths of the songs or phrases in seconds, and multiply by the number of times the bird sings per minute, hour, and day, and take into account also the length of the song season, we find that the poorest singers do not have any such total output as the melodious singers. Many of the former sing less than one-fourth of each 60-second period, even when singing as steadily as they ever do. In addition, they tend to confine their singing largely to the breeding season, whereas many good singers perform both continuously and, as several writers have noted (Craig, 1943: 152–153; Zimmer, 1919), for an unusually large portion of the year. For example, Carolina Wrens and Mockingbirds are heard almost daily in the Atlanta area for twelve and nearly eight months, respectively. Out of 21 singers in the United States that seem to have been judged to have the most highly developed songs (I have heard 17 of them), eight sing most of the year, or, allowing for continuity, perhaps nearly three times the average total (taking data chiefly from Saunders' careful accounts of New England species); six sing at least 50 per cent more than the average; and the remaining seven have at least average outputs. This is hardly a chance distribution. In England, taking Nicholson and Koch's list (1936: 1, 70) of the songsters with the most "power and variety," five are permanent residents, and these (according to Nicholson's "calendar") sing on the average nearly eight months of the year, some of them very continuously (in each performance period), implying a total of more than twice the average output. The other five are migrants, and these sing at least the normal

amount while in England (the Nightingale making up through continuity and extra night singing for its short season). In addition, all but one (the Marsh Warbler, *Acrocephalus palustris*) are said to sing a good deal when wintering in Africa or while migrating. Again we have a decided correlation. In the Piedmont Plateau of Georgia, where I write, of the five good songsters wintering near our house (Mockingbird, Carolina Wren, White-throated Sparrow, Brown Thrasher, *Toxostoma rufum*, and Cardinal, *Richmondena cardinalis*) the first three sing freely much of the autumn; on the other hand, the five poor or mediocre singers (Towhees, *Pipilo erythrophthalmus*; Blue Jays, *Cyanocitta cristata*; titmice and chickadees, *Parus bicolor* and *P. carolinensis*; Flickers (*Colaptes auratus*) are almost songless from September to January. Nor do they "make up for the lost time" by resuming their singing correspondingly earlier in February or March.

The interest of this principle is that it constitutes evidence that our human classification, "good singer," has some biological meaning, since our enthusiasm for the performance of such a singer is matched by the performer's own more intense interest in it. He does not drop the activity the moment the climax of the life cycle is over, but continues it much longer, or nearly all the year; he does not spend most of a performance period in intervals of silence but sings as though, for the few minutes, or perhaps half an hour or more, singing were life itself. Naturally, if we use continuity as one criterion of quality as well as of quantity, our generalization becomes in part tautological; but only in part, since there are other criteria on both sides. The further fact that birds act as though to avoid monotony in their singing (principle 3), and sing as much during a performance period as this avoidance permits (principle 4), also gives some support to the view that they do in their way experience musical enjoyment, as does the evidence which imitation furnishes that they attend to the sounds they are making, and guide their utterances partly by their auditory impressions. Further, the standard explanation of harmony, first given by Helmholtz, I believe, is such as, in its simpler aspects, to apply to birds as well as to man; and as much can be said for explanations of the simpler effects of rhythm and melody. (Statements sometimes made that birds lack some elementary factor of musical utterance seem due to inadequate experience; somewhere in the world a bird turns up [or several] which exhibits the missing factor, provided it be not too elaborate or complex.)

The most notable exception I have heard of to the present principle is the Cactus Wren (*Campylorhynchus brunneicapillus*), an unmusical singer said to sing incessantly and all year. However, what total output is indicated by "incessantly" one can only guess. Another, opposite kind of apparent exception, from nearly the same desert region, is Leconte's Thrasher (*Toxostoma lecontei*), which sings a "musical" and powerful, yet "infrequent" song

(Hoffman, 1927:251; Peterson, 1941:137). It may be that this species is losing the tendency to sing, owing perhaps to extreme heat much of the day, or the high visibility of its habitat (see principle 9, below).

7. The Unequal Distribution of Musical Ability by Families

Since families represent specialization (some more than others), principle 2 should lead us to expect the present generalization. The crow family (Corvidae) has few even third-rate songsters, and no nearly first-rate ones, and this is true of a number of families. By contrast, the thrush subfamily has about 80 first-rate musicians, and the proportion in the wren family (Troglodytidae) is nearly the same (not far from 30 per cent). In the thrasher–mockingbird family (Mimidae) at least half are outstanding songsters. These dramatic differences are not plausibly ascribed to chance (see below, principle 9) or to bias or ignorance in my classification of species as outstanding musically (based on descriptions and, in representative samples, direct experience, at least of recordings). Nor are the differences very closely correlated with those in physical vocal equipment, since, for example, crows are well endowed in this respect (Miskimen, 1951).

8. The Relatively Equal Geographical Distribution of Musical Ability

Compared to the extreme contrasts between families, the geographical differences are unimpressive, if we rule out regions where species of perching birds are lacking or few, such as extremely cold, arid, or barren regions. The sometimes-maligned tropics, for example, contain about half the world's most highly musical species (the evidence for this must be reserved for another occasion), and yet the tropical areas total but one-third of the land surface of the globe. There are marked unevennesses in the distribution of good tropical singers, but every considerable region has some.

This universality of musical utterance, the world over, and in many widely-different families, shows how deeply grounded in bird life the phenomenon is. That there are everywhere some strikingly unmusical songs among oscinine birds may indicate that if, by chance, a species hits upon a distinctive, penetrating, but harsh utterance, there may not be much to gain by its transformation into a musical one. Examples: the Ovenbird (*Seiurus aurocapillus*), or the Australian Wattlebirds (genus *Antochaera*).

9. The Ecological Distribution of Musical Ability

The degree of musical development (measured by variety, purity of musical tone, pitch span, carrying power) tends to be correlated positively with most, if not all, of the following factors:

(a) Relative invisibility, as due to habitat (dense vegetation, clouds or fog), dull or protective coloration, smallness of size, secretive mode of life (flying swallows or hawks can usually see one another);

(b) Lack of sexual dimorphism;

(c) Degree of territorial possessiveness, and (up to a point) size of territory (hence, species which are gregarious in the breeding season are poor singers);

(d) Number of closely-related, especially like-sized, songbird species within hearing of one another;

(e) Scarcity of strong-voiced, primitive forms, such as parrots, cuckoos, toucans, doves, which, when abundant, may make such a racket that musical qualities tend to be imperceptible;

(f) Audibility as due to habitat (Beebe and others have thought that certain tall tropical forests, as in northern, lowland South America, absorb delicate sounds and put a premium upon harsher ones—see *e*, above);

(g) Efficiency of feeding methods, yielding surplus energy and time;

(h) Mild weather over much of the year.

As to (*a*, *b*), since song is vocal signalling, the need for it must be partly proportional to the ineffectiveness of visual cues; also, since song is above all territorial "advertisement," strong territorial habits (*c*) make signalling necessary for long periods of time and not merely during courtship, and over considerable distances, with the consequence that signals must be not only loud but distinctive enough to stand out, not simply from a few nearby sounds, but also from the more varied assortment coming from a greater distance. They must be different from mere calls, which tend to be alike in both sexes and sometimes in related species and which do not differentiate between an individual occupying a territory and one not so doing, but perhaps travelling in a flock. The number of like-sized species (*d*) in an area, especially if they are congeneric or of the same family, increases the need for distinctive patterns, rather than mere shrieks or chirps which tend to betray only the size and basic structure of the species.

Though the presence of many types of songbirds in an area is probably favorable to song-development, the presence of many primitive forms with unmusical voices (*e*) may be unfavorable. At dawn, especially, a critical time, it may be hard for the more exquisite voices to make themselves heard. Some observers with tropical experience doubt the validity of the argument. Yet we do need an explanation for the rather low yield of the Amazon Valley in musical species, even among Oscinines, compared to the highlands of Central America, Colombia, Africa, or Java. Possibly the tendency of lowland tropical birds to follow ant-armies, with resultant weakening of territoriality, is a factor. Possibly there are too many species, even of songbird

type, in the Amazon. Is there a saturation point in number of different songs that can be effective? Compare the hopeless confusion of sounds in bird houses in zoölogical gardens. On the other hand, the number of individuals in an area is not necessarily much greater in the tropics. It has been suggested by Keith Dixon that, as in trees, birds of tropical rain-forests may be thinly distributed, and thus mutual stimulation within species is diminished and the territorial functions of song reduced. Perhaps (as Professor Pettingill has suggested) the year-round combination of high humidity and fairly high temperature in lowlands along the equator inhibits song. The sound-absorbing character (*f*) of tropical forests perhaps differs from that of other forests. In any case birds of most tropical areas are fairly musical. As to (*g*), insectivorous birds may have an advantage (especially compared to those living chiefly on small seeds) in the high protein content of their food, and ground feeders have a further advantage, perhaps, in that worms and grubs are more rewarding than small flies, mosquitoes, and aphids. Or is walking or hopping on the ground more economical of energy than some other methods of locomotion while feeding? The enormous superiority of thrushes, musically speaking, to even the Old World flycatchers (nearly 30 per cent outstanding singers, compared to about 1 per cent), is strongly suggestive, though it may also be true that the flycatching habit makes the bird more visible to its fellows (*a*). Ground-feeding in forest or long grass also means relative invisibility, and this may well be the main point. There seems little doubt that ground-feeding does favor song (principle 5 is probably relevant here). Thus ground-feeding members of the Parulidae include nearly all of the loudest and most of the more musical songsters in this family. For instance, the two chats (*Icteria virens* and *Granatellus venustus*), the Ovenbird and the water thrushes (genus *Seiurus*), and Swainson's Warbler (*Limnothlypis swainsonii*) may be cited.

(h) Mild weather releases more energy for song, and mild weather for much or all of the year—by stabilizing the food supply and eliminating the necessity for migration—increases the opportunity (Robinson: 1949, 1956) to perfect complex types of singing, which to some degree have to be learned (see Principle 11). Perhaps this is why, in the far North, while some species sing sweetly, there is a lack of complexity and variety of singing. (The prolonged daylight, however, in part atones for the shortness of the season.)

Of the ecological principles, (*a*) and (c) are probably the most important, and certainly they are the ones most securely established by known facts. Colonial nesters, and gaudy, conspicuous birds living in well-lighted places, are not good singers; the typical songbird is, like the usual thrush or wren, a highly territorial form, feeding in dark substages of forests or thickets, with somber, protective coloration.

10. Sex Distribution of Musical Ability in Relation to Climate

The potentiality of song is innate in both sexes in many, possibly all, species, but is for the most part inhibited in the female under natural, and to a lesser extent artificial, conditions (as in caged birds), with the partial and notable exception that in tropical and subtropical areas scores, very possibly hundreds, of species exhibit female singing as a normal part of the life pattern. It often takes the form of "dual singing," antiphonal singing, or "duetting," according as the female sings a portion (usually, or perhaps always, the last) of a single unitary pattern, or replies to the male song with one of her own, or sings simultaneously with the male. The functions of such joint singing include that of maintaining the pair bond throughout the year. It is scarcely a mystery that the luxury of female singing occurs chiefly in uniformly mild climates, where migration and the struggle with severe cold are both absent. There is an additional, though I judge much less frequent, form of female song where winters occur but are not very severe, as in Britain and the southern United States: this is singing by females occupying individual winter feeding territories of their own, Robin Redbreast (*Erithacus rubecula*), Mockingbird. Female song as standard behavior occurs in many parts of the world (for instance, Mexico, Africa, Australia) and in widely-different families, but only, so far as I know, in non-migratory, and usually sub-tropical or tropical, species. It is then definitely associated with climate, plus some as yet undetermined factors.

11. Innately Guided Imitation and Learning

Evidence is accumulating that the songs of most, possibly all, species result from an inborn tendency toward the specific type of song, always, however, more or less influenced in its maturing by practice and by hearing songs sung by other individuals. Usually these individuals are of the same species but, in exceptionally imitative forms, or in captivity, of other species as well. It has yet to be strictly proved (and seems unlikely) that *any* species is wholly without innate disposition to sing a characteristic song; for it is not enough to show that, given early and exclusive exposure to a "foreign" song, the species will sing this foreign song rather than that of its species. One could only conclude from this that the exposure is a stronger force than the innate trend, if the latter exists. To prove the absence of such a trend one must show that, given exposure to no adult singing (nurtured in a sound-proof chamber), the individual will still not sing its proper song. This has been tried with the Chaffinch (Thorpe, 1954) and two other species (Sauer, 1954; Messmer and Messmer, 1956). The Chaffinches did sing the proper song; although, when other individuals of the same species were exposed solely to foreign songs, they adopted them and failed to sing the song of their own species. Further, when several distinct groups were brought up in isolated

chambers, each group developed its own version of the song of the species, thus beautifully showing the blend of innate and imitative factors. The other two species also sang correctly, although when examples were provided they always were responded to in some degree. Very likely all species have something innate and (in the wild) something learned in their singing—learned at least in the sense of perfected by practice, and probably also in the sense of having been influenced by the hearing of other individuals. The proportions of the three factors doubtless vary greatly in diverse species, and slightly in diverse individuals. Song apparently sums up nearly that a bird is, both of instinct and of plasticity or "intelligence." Birds are innately musical, as man is innately talkative, for as babies babble in speech-like sounds, so young birds (though within much narrower grooves of instinctive pattern) "warble," in rambling, exploratory fashion. That imitation plays a role, often an important one, and that songs develop with practice, show that birds are aware of, and in a manner judge, their musical efforts (Howard, 1952:177–199). Such judgment works within narrow limits, but it probably has something in common, though at a vast removal, with man's musical intelligence.

12. The Possible Light–Dark Influence Upon Exuberance

This idea, suggested by L. A. Fuertes (1914), is highly speculative, not to say nebulous, and scarcely susceptible of proof. The "gayest," most exuberantly joyous, songs are thought to occur in species living in the open sunlight, and the least gay, or the most solemn, plaintive, or "chaste" songs to characterize forest-dwelling forms, living in dense shade. In the United States, exuberantly joyous songs are those of: the Bobolink (*Dolichonyx oryzivorus*); American Goldfinch (*Spinus tristis*—a name referring evidently to the call notes, not the song); the House Finch (*Carpodacus mexicanus*); the Purple Finch (*Carpodacus purpureus*); the Western Meadowlark (*Sturnella neglecta*); Townsend's Solitaire (*Myadestes townsendi*); and the House Wren (*Troglodytes aedon*). Most of these live entirely, and all of them to some extent, in the sunshine, in well-lighted places. The songs perhaps most solemn or chaste are of the Varied Thrush (*Ixoreus naevius*); the Veery (*Hylocichla fuscescens*); the Wood Thrush, the Hermit Thrush (*Hylocichla guttatus*); the White-throated Sparrow; the Wood Peewee; the Eastern Meadowlark. Of these, only the last lives in anything like bright light; and perhaps not even it does in comparison with the Western Meadowlark, since, before the forests were felled, it must have often frequented partly-shaded stream valleys or grassy areas surrounded by forest; and it also inhabits the cloudier and moister parts of the continent, where the growth of grasses is taller and denser, affording more shade (Lanyon, 1956: 103–105). In England, the Skylark (*Alauda arvensis*) is an exuberant singer, while its relative, the Wood Lark, is decidedly chaste, and as its name indi-

cates, and I believe in fact, it lives more in the shadow of trees. (The contrast between Meadow and Tree Pipits, *Anthus pratensis* and *A. trivialis*, is less easily fitted into the scheme.) The Chaffinch (*Fringilla coelebs*) is also rather gay, and it lives largely in somewhat open places; while the Blackbird (*Turdus merula*), the nightingales (*Luscinia*), and the British Robin are apparently typical chaste forest songsters. Birds living much in tree tops, as do many warblers (Sylviinae), are intermediate in relation to sunshine, and so perhaps are their songs. It might of course be argued that our own impressions of the "gaiety," or the opposite, of the songs are largely determined by the environment in which we find them. But this would be an exaggeration. There are objective characteristics of "gay" music (rapid tempo, for one), and they are found in high degree in the Bobolink, for instance, and not at all in the Varied Thrush or the Veery, which seek the deep shade and are among the most solemn of our birds. Also, no one ever thought the Eastern Meadowlark, or the Vesper Sparrow (*Pooecetes gramineus*) particularly gay, yet these occur in our experience together with sunshine. (Both seem exceptions to the Fuertes principle, if it be a principle.) We may imagine that species which, for food-getting reasons and/or security, live in subdued light, and therefore have an instinctive preference for such conditions, may also have a bent toward subdued ways of feeling and acting. The forest thrushes not only have more solemn songs, they have perhaps a more solemn comportment than many dwellers in the open. Possibly (here again I am indebted to Dr. Pettingill) "chaste" songs carry better in the forest than other songs. In one way or another, then, there may be something in Fuertes' idea.

These are some of the reflections to which 40 years of attention to a delightful aspect of nature have led me. Even to begin to justify them would require assembling a great mass of facts, and the writing of a book. I hope to write this book. But meanwhile, it seems appropriate to invite others to join in the game; for numerous observers must know many relevant facts of which I am not aware. I have always believed that there must be laws in this area. If the foregoing are not the right ones, what should be put in their place? There must be elements of discoverable order in these matters.

Summary

The proposed generalizations or "principles" are as follows:

1. Class limitation, as determined by structure.

2. Species Limitation, or Exclusive Specialization: the impossibility that a species should excel in all the capacities of its class.

3. Minimum Versatility, or the Monotony Threshold: mutual exclusiveness of repetitiveness and continuity.

4. Maximal Continuity, or (in combination with the preceding) the positive Correlation of Continuity and Versatility.

5. Spatial Detachment of Continuous Singing from Feeding.

6. Correlation between Quantity and Quality: better singers produce more song.

7. Unequal Distribution of Musical Ability by Families.

8. Relatively Equal Geographical Distribution.

9. Ecological Distribution according to: invisibility; sexual monomorphism; territoriality; number of Oscinine species in the area; scarcity of strong-voiced, primitive species, sound-transmitting characteristics of the habitat; efficiency of feeding methods; mild weather.

10. Sex distribution according to Climate (female singing integral to the life-pattern of a good many species not subjected to cold weather or migration).

11. Innately-guided Imitation and Learning.

12. Possible Light–Dark Influence upon Exuberance in Song.

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PAIRING BEHAVIOR OF PIGEONS RELATED TO AGGRESSIVENESS AND TERRITORY[1]

BY PAUL L. CASTORO AND A. M. GUHL

EXPERIMENTATION with pigeons and doves in the field of social behavior is complicated by the fact that the social organization is based on peck-dominance (Masure and Allee, 1934; Bennett, 1939) or bidirectional pecking, whereas peck-right occurs in many other birds (Allee, 1952). The peck-right pattern permits a more stable social organization, as the order of ranking individuals under bidirectional pecking is fluid. Experimentaton with Ring Doves, *Streptopelia risoria* (Bennett, 1940), presented difficulties in analysis since some control individuals shifted ranks in the social hierarchy.

Ritchey (1951) noted definite territories among Common Pigeons (*Columba livia*), and suggested a positive correlation between the percentage of encounters won and the amount of territory defended. She concluded that territorialism blocked a rigid dominance hierarchy such as is found among Domestic Chickens (*Gallus gallus*). Bennett (1940), Diebschlag (1941) and others previously suggested that territoriality plays an important role in the establishment of a dominance order. In unisexual groups of the Common Pigeon, each individual defended a portion of the perch upon which it was usually found. Under such conditions territoriality was reduced to what may be called a perch-right. The exchange of pecks between any two individuals showed a balance in favor of the one nearest the center of its territory.

The object of this experiment was to determine if there was any relationship between relative aggressiveness in pigeons and sexual behavior. Among chickens, high ranking cocks sired the most chicks and had precedence in mating (Guhl and Warren, 1946; Guhl, Collias and Allee, 1945), and receptivity in females showed a negative correlation with social rank (Guhl, 1950). To determine whether social dominance or levels of aggressiveness influence sexual behavior, particularly pairing behavior, in pigeons it was necessary to devise a method of evaluating the aggressiveness of the individuals without the influence of perch rights.

The courtship display, pre-mating display and other behavior patterns in pigeons have been discussed in the classic work of Whitman (1919), and also by Craig (1918) and Gifford (1941). Courtship display is usually performed by the male, and shown by the fluffing of the breast feathers, dragging of the tail, cooing, and treading of the feet on the floor. If the female is receptive she will nod her head, after which billing follows. The male presents an open beak into which the female inserts hers. There is evidence that the male regurgitates into the beak of the female. Subsequently the female will crouch, elevate her wings and receive the male, and the pair-bond is formed.

[1] Contribution No. 320, Department of Zoology, Kansas State College.

Experimental Methods and Procedure

The pigeons used in this study were obtained from a farm house near Manhattan, Kansas. Of the 45 birds trapped, 11 males and 13 females were selected on the basis of equality of size and the appearance of good health. These were treated with five per cent chlordane powder to eliminate any ectoparasites.

To determine the sex of the individuals, a method similar to that described by Lee (1915) was used. The male is usually larger and heavier than the female and his pelvic bones are closer together and more rigid than those of the female. Mr. Herman Smith of the Department of Poultry Husbandry tried to obtain semen by methods used for artificial insemination in poultry, but this did not identify all of the males. As a further test for sex the birds were all placed into a small cage for two days, and observed for sexual behavior. As the sex of each bird became evident, it was removed and placed into a cage with others of the same sex.

For identification of individuals each bird received a numbered and colored legband, red for males and green for females.

Several types of cages were used and are described below. During certain tests the birds were kept as unisexual groups in cages designated as the "home cage." Tests for aggressiveness were made in a "combat cage" and those for pairing behavior in a "pairing cage." Finally the sexes were brought together in a "flight cage."

The Home Cages.—The males and the females were in separate cages of similar construction, measuring 6 x 4 x 2 feet. In these cages the birds could move about quite freely but could not fly. There were many interactions among the males and they tended to space themselves and to remain within a certain area. The females showed little aggressive activity and scattered indiscriminately. The pigeons were in these cages for 40 days, during which time they ceased to recognize former mates. According to Carpenter (1933) pigeons will forget their mates after about 24 days. Although there was a tendency, especially among the males, to defend certain areas, it was doubtful whether these relationships carried over into the test situations as the combat cage provided a strange area, the rights over which had to be won.

The Combat Cage.—The object of this cage was to induce fighting behavior, the results of which would indicate some measure of relative aggressiveness. The birds were introduced into the cage by twos until each bird had met and settled dominance relations with each of the others of its sex. This procedure is a modification of the initial encounters staged by Collias (1943) for chickens. Individuals were ranked in levels of aggressiveness according to the number of such encounters won. This procedure has proved to be satisfactory (Guhl, 1953) for chickens.

The combat cage was made of chicken wire on a wooden base. It was circular, 13 inches in diameter and 8 inches high. This size and shape allowed the birds to be intimately close at all times with no corners in which to take refuge.

Two pigeons of the same sex were taken from the home cage and introduced simultaneously into the combat cage. The observer then retired behind a screen. After a short interval the males began to fight, but the females had to be stimulated by presentation of food, after being deprived of food for about 24 hours in the home cage.

The Pairing Cage.—This cage was constructed similar to the combat cage but somewhat larger, being 24 inches in diameter and 12 inches high. Each male was introduced into this cage with two females, to determine whether pairing behavior may be related to the relative aggressiveness of the females.

The Flight Cage.—This cage was 6 x 5 x 7 feet. It was built against one wall of the laboratory; two other sides were made of chicken wire netting and the fourth side, or end, was composed of 10 large nest boxes. Perches were constructed near the end opposite the nest boxes. Containers for food and water were placed on the floor.

After the tests for pairing behavior were completed, all the males were placed into the flight cage and permitted to establish territories. The females were then tested singly in the flight cage to determine whether levels of aggressiveness of the males could be related to success in pairing when in competition with other males. As soon as pairing was effected the female was removed and returned to the home cage. Three days elapsed before another female was introduced. After these observations were completed all the females were introduced simultaneously and subsequent pairings were noted.

Observations and Results

Determination of Relative Aggressiveness

The Males.—When two males were placed into the combat cage, one would usually begin to display immediately. A typical display included the fluffing up of feathers of the neck region, dragging of the tail feathers on the floor, treading with the feet, and loud vocalizations. The reactions of the other bird were either positive or negative. In the latter response it would avoid the bird in display, which was then considered the winner of the contest as he established dominance. The length of time required to settle dominance relations varied with the intensity of actions and reactions. Dominance was considered as established when one bird displayed aggressively and the other showed avoidance and maintained such a reaction. A bird assuming the subordinate status would lower his head and tend to carry the long axis of his body in a nearly horizontal position, whereas the dominant one would maintain a stance in which his body would be nearly erect and his head held high. If a subordinate bird raised his head, he invariably would be pecked.

A bird which reacted positively to the one displaying would deliver a series of pecks, and usually a fight ensued. In fighting there was an exchange of pecks and wing slapping with loud vocalizations. During intensive fighting one male grasped the other and tried to shake him. Eventually one of the contestants showed escape or avoidance behavior, which often was intense under such confined conditions. The birds were returned to the home cage as soon as the observer judged that a decision had been reached. Some contests ended in "no decision" even after one hour. In one case the males fought repeatedly without either giving way; in others neither aggressive nor submissive behavior was shown.

Each bird met each of the other males in a systematic manner. Three rounds were made for a total of 330 pair contests. A summary of the results is given in Table 1, which shows the number of individuals that each bird

TABLE 1

RESULTS OF CONTESTS BETWEEN PAIRS OF MALES IN THE COMBAT CAGE
MALES ARE RANKED ACCORDING TO NUMBER OF INDIVIDUALS EACH DEFEATED

Winners	Losers										Number defeated	Rank
6	7	5	2	3	9	13	1	10	11	8	10	1
7		5	2	3	9	13	1	10	11	8	9	2
5			2	3	9	13	1	10	11	8	8	3
2				3	9	13	1	10	11	8	7	4
3					9	13	1		11	8	5	5
9						13	1	10		8	4	6.5
13							1	10	11	8	4	6.5
1								10	11	8	3	8
10				3					11		2	9.5
11					9					8	2	9.5
8								10			1	11

defeated in these contests. The bird listed in the first column gained dominance in two or three contests with each of the birds given on the same horizontal line. The numbers are those of the legbands. The relative aggressiveness of each male is indicated by the number of individuals it dominated, and the last column gives the ranks in aggressiveness. It should be emphasized that these measures of aggressiveness are relative only to others in the same group and can not be used for intergroup compairisons. The ranks were later used to determine the influence of relative aggressiveness on pairing behavior.

The Females.—Encounters by female couples in the combat cage were conducted like those for the males, with one exception. Female pigeons are not as aggressive as the males, and food competition was used to induce aggression. Food was withheld from the females in the home pen for about 24 hours prior to the contests; and a small cup of food was fastened to the floor in the center of the cage. When two hungry females were introduced into the cage, both fed simultaneously until most of the food was gone. Fighting began with the competition for the last few grains. Except for display, the encounters were similar to those of the males. There was slight fluffing of the feathers on the neck and a very mild vocalization. There was no treading of the feet or dragging of tail feathers as observed among the males.

Three rounds of paired encounters gave a total of 468 contests. The results are summarized in Table 2 in a manner similar to that in Table 1. It may be noted that in both sexes there were deviations from a straight-line ranking of aggressiveness; This condition may have resulted from variables during the contests or it may reflect statistical phenomena of minor, unmeasurable differences in aggressiveness.

TABLE 2

RESULTS OF CONTESTS BETWEEN THE PAIRS OF FEMALES IN THE COMBAT CAGE
FEMALES ARE RANKED ACCORDING TO THE NUMBER OF BIRDS EACH DEFEATED

Winners	Losers												Number defeated	Rank
12	14	22	20	18	23	15	21	19	16	17	25	24	12	1
14		22	20	18	23	15	21	19	16	17	25	24	11	2
22			20	18	23	15	21	19	16	17	25	24	10	3
20				18	23	15	21	19	16	17	25	24	9	4
18					23	15	21		16	17	25	24	7	5
23						15		19	16	17	25	24	6	6
15*							21	19		17	25	24	5	8
21*					23			19	16		25	24	5	8
19*				18					16	17	25	24	5	8
16						15				17	25	24	4	10
17							21				25	24	3	11
25												24	1	12
24													0	13

* These birds tied for the same position on the aggressive scale.

MATE SELECTION IN THE ABSENCE OF TERRITORY

Territory plays an important role in pairing and nesting among pigeons. Within the pairing cage there was no established territory. A male and two females were placed simultaneously into this cage and pairing behavior was observed. The relative aggressive ranking of all three birds was used to determine whether levels of aggressiveness exerted any influence on pairing behavior. All three birds were returned to their respective home cages after a pair-bond had been formed.

Only 28 pair-formation tests were made out of a possible combination of 1716 (if each of 11 males were tested with each of the 156 possible female couples). Each male was used at least once and two were used five times. Each female was member of a couple at least two times and one was used 15 times. In four instances the same pair of females was used with two or three males.

The reactions of the three birds usually followed a typical pattern. The male began to display immediately, directing his advances to either of the females, and this continued for about 15 minutes. The dominant female maintained an alerted stance. Subsequently the subordinate began bobbing or nodding her head. This sign of receptiveness was followed by attempts to copulate. At times the dominant female would attack her inferior and thereby prevent copulation. After billing ensued, copulation was successful and the pair-bond was established. Thereafter the mated pair preened or

began to attack the unmated female, apparently in an effort to establish a nesting territory. At this point the test was considered to be concluded and all three birds were removed.

The results of the 28 tests are given in Table 3. The data are grouped according to the degrees of differences in the ranking of the females. In the first group these differences are neither very great nor very small. In the second group all the females have the same rank, that is, they were tied for rank number eight (see Table 2). The next group includes pairs of females with wide differences in rank. Then follow two tests in which both females were ranked high in aggressiveness, and in the last three tests both were relatively low in rank.

The legband numbers for the females with which the male paired are printed in bold face type. In all but two tests the pair-bond was established with the female of lower rank in aggressiveness. In these instances number 17 dominated number 21 and 21 dominated 23 (Table 2), in the combat cage and probably in the home cage. Similarly for the pairs in which both females tied for rank eight, the one selected by the male was the subordinate. It did not seem to make any difference in the results whether the paired females were both of relatively high or low rank, or of wide separation in rank. In those tests in which different males were used with the same pair of females, all the males selected the same female. These results and the observations recorded indicate that sexual behavior was facilitated by the submissive stance of the female, and that synchronization of the sexes was influenced by the submissiveness of the female and the aggressive posturing of the male.

Establishment of Territories by the Males

The 11 males were placed into the flight cage as a group and permitted to establish territories. The nest boxes, at one end, were a stack of five orange crates, with each half suitable for a nest. There was some space beneath the bottom nests and the floor. Straw was provided for nesting material. Two perches, at a height of about five feet, were situated near the opposite end. For about one hour the birds flew about in confusion, and then began to select nest boxes. There appeared to be a shifting of perching sites. Some would leave a box for no apparent cause; others would be attacked and driven out; and still others would defend their holdings. This scene of turmoil lasted for about five days. Several more days passed before the territories became more stable.

Seven of the 11 males established territory in nest boxes; two selected sites on the floor under the nest boxes; one elsewhere on the floor, and male number 8 (rank 11) remained on one of the perches. There was no indication that level of aggressiveness had any relation to the nest box selected, which may mean that the location of a nest box had no obvious advantage under these

TABLE 3

RESULTS OF TESTS ON PAIRING BEHAVIOR

FIGURES IN PARENTHESES ARE THE RANKS IN RELATIVE AGGRESSIVENESS

(Legband numbers in boldface indicate the female selected by the male in pairing.)

Male		Dominant female		Subordinate female	
Number	Rank	Number	Rank	Number	Rank
1	(8)	18	(5)	**16**	(10)
3	(5)	18	(5)	**16**	(10)
2	(4)	15	(8)	**16**	(10)
3	(5)	15	(8)	**16**	(10)
6	(1)	18	(5)	**15**	(8)
6	(1)	18	(5)	**15**	(8)
13	(6.5)	18	(5)	**15**	(8)
10	(9.5)	14	(2)	**19**	(8)
11	(9.5)	20	(4)	**19**	(8)
13	(6.5)	20	(4)	**21**	(8)
9	(6.5)	23	(6)	**24**	(13)
8	(11)	**21**	(8)	17	(11)
9	(6.5)	23	(6)	**15**	(8)
3	(5)	**23**	(6)	21	(8)
13	(6.5)	15	(8)	**19**	(8)
8	(11)	15	(8)	**21**	(8)
11	(9.5)	15	(8)	**21**	(8)
13	(6.5)	21	(8)	**19**	(8)
6	(1)	12	(1)	**25**	(12)
7	(2)	14	(2)	**25**	(12)
9	(6.5)	23	(6)	**24**	(13)
8	(11)	12	(1)	**17**	(11)
9	(6.5)	14	(2)	**17**	(11)
3	(5)	14	(2)	**22**	(3)
5	(3)	22	(3)	**18**	(5)
3	(5)	16	(10)	**25**	(12)
6	(1)	15	(8)	**25**	(12)
9	(6.5)	15	(8)	**24**	(13)

conditions, or that trial and error and chance determined the site finally accepted.

COMPETITION FOR A MATE BY TERRITORY-HOLDING MALES

When the male territories were firmly established the females were introduced singly and allowed to remain until a pair-bond had been formed. Under these conditions pairing required two or more days and the high level of activity kept the males from feeding. After the female was removed a lapse of three days occurred before another female was introduced.

The behavior was usually as follows. Several males flew to the female and attempted to display. At first the males were more intent on display than on

fighting with competitors. During this excitement the female flew between the nest boxes and perches, always pursued by some males. Territory boundaries were violated and fighting ensued. The number of males remaining in the competition gradually decreased. If the female tended to remain within a certain territory, that male possessed some temporary advantage. The male that won her attention had the problem of driving the female to his nest box and keeping her there. This he would do in manners described by Whitman (1919), such as flying between her and his nest box, nudging her, pulling on her feathers, and giving the nest call. Once she was in his nest he would begin the courting display. With the onset of billing and copulation the pair-bond was formed, and both would take part in defending the nest territory.

TABLE 4

PAIR-BONDS FORMED BY EACH MALE WHEN FEMALES WERE INTRODUCED SINGLY INTO THE FLIGHT CAGE

(Numbers in parentheses are ranks in relative aggressiveness)

Males Number	Rank	Females with which males paired					
6	(1)	25 (12)	21 (8)	19 (8)	14 (2)	17 (11)	12 (1)
7	(2)	23 (6)	18 (5)	15 (8)			
5	(3)	24 (13)					
2	(4)						
3	(5)	20 (4)	22 (3)				
9	(6.5)						
13	(6.5)						
1	(8)						
10	(9.5)	16 (10)					
11	(9.5)						
8	(11)						

The results for the 13 females are given in Table 4, in which the legband numbers are given for each male and each of the females with which he paired. The numbers in parentheses are ranks in relative aggressiveness. The top three males in levels of aggressiveness paired with 10 of the 13 females. The indications are that the aggressiveness of a male gave him an advantage in securing a mate under competition with other males. There was no evidence that the relative aggressiveness of the females had any definite relation to that of the male with which she paired. However the aggressiveness of the females seemed to have some influence on the synchronization, as low-ranking females paired within two days whereas high-ranking females required from five to nine days to pair.

RELEASE OF FEMALES INTO CAGE WITH GROUP OF MALES

In the final phase of this experiment, 12 females were placed into the flight

cage containing 11 males with established territories. Female number 12 was not included as she had been in the flight cage two days previously, and it was believed that she might return immediately to the male with which she had paired.

As the females entered the cage, the males immediately started to fly wildly and began to display vigorously. The females were pursued and territorial rights were ignored. The top ranking male, number 6, displayed to a number of females, whereas other males appeared to single out specific females. For two days there was so much activity and calling that the observer could not determine whether a given female was responding to the calls of a particular male. It appeared as though pairings which occurred were largely a matter of chance.

TABLE 5

PAIRS FORMED AFTER THE FEMALES WERE INTRODUCED, AS A GROUP, INTO THE FLIGHT CAGE CONTAINING THE MALES

(Figures in parentheses indicate rank in aggressiveness)

Day	Male		Female	
	Number	Rank	Number	Rank
I	8	(11)	17	(11)
	11	(9.5)	15	(8)
	10	(9.5)	16	(10)
II	2	(4)	20	(4)
	1	(8)	25	(12)
III	7	(2)	18	(5)
IV	5	(3)	22	(3)
V	13	(6.5)	19	(8)
	6	(1)	21	(8)
VI	9	(6.5)	23	(6)
	3	(5)	14	(2)

The results given in Table 5 are the pairings as listed by days on which the pair-bonds were established. There was a tendency for low-ranking birds to pair earlier than high-ranking ones, particularly among the males; and no relationships between levels of aggressiveness of mated birds can be considered with confidence. The data in the table tempt one to draw conclusions which would not be warranted by the behavior observed.

DISCUSSION

In testing for relative levels of aggressiveness a method similar to that developed by Collias (1943), for chickens, was used. One major difference was that Collias used birds which were strangers, whereas the pigeons used here were caged in unisexual groups and therefore were not strangers. However, chickens are not territorial and pigeons are, in that they have perching

areas and nest areas which they defend. It was assumed that two birds, whether acquainted or not, would fight in a strange location to establish area rights. The fact that definite dominance–subordination relations were established suggested that the use of a combat cage permitted the measurement of aggressiveness. If this method is repeated one might isolate the individuals in the home cage with screened partitions, to eliminate the possibility of home-pen effects, if any. Some observations in this experiment suggested that dominance relations in the home pen showed some agreement with the outcome of pair-contests in the combat cage. This may not necessarily reflect seriously on the ratings of aggressiveness as Guhl (1953) obtained high correlations between ranks in a peck-order of chickens and ranks in levels of aggressiveness measured by initial pair contest, i.e., between strangers.

Whitman (1919) defined the mating period as the activities of the reproductive cycle which begin with courting and end with the laying of the first egg. This may be considered as the activities leading to and including the establishment of a pair-bond. With poultry the term mating is usually used for coition since these birds are promiscuous and do not form pair-bonds in the usual sense. According to Whitman the mating period in pigeons embraces courting, copulating, and the hunting, acceptance and construction of the nest. Its duration is six or seven days. Copulation is intermittent throughout the mating period. Both males and females may extend their state of readiness in the sexual cycle for a month or longer if separated. The primary sex impulse may arise relatively automatically. Once a cycle has begun it tends to run its course. Unisexual pairs may stimulate each other to begin the cycle, even to laying by females. As far as could be determined the birds in the home cages were in the state of readiness, for no eggs were laid and pair-bonds were formed in the pairing cage. The relatively crowded conditions and the limited vertical range probably facilitated the maintenance of the state of readiness. In a large flight cage or in freedom, individuals would be expected to vary in the phases of the cycle and certain sex pairs might not synchronize. It may therefore be concluded that the results obtained here, i.e., that the male paired with the subordinate female, was not due to lack of readiness of the dominant one. Furthermore a given dominant female would pair when matched subsequently with one of her superiors in the pairing cage. It should also be noted that the tested birds were removed before the mating period (as defined by Whitman) was fully established; this action therefore maintained a state of readiness.

It was apparent that the male reacted to the display of submissiveness, a crouch-like stance, and not to dominance status. It has been shown in chickens that low-ranking hens crouch more readily for a cock, and that high-ranking hens will show more receptivity when their habit of domination is reduced by removing most of their subordinates (Guhl, 1950). Unisexual

matings were also related to dominance in hens (Guhl, 1948) and cocks (Guhl, 1949; 1953). Unisexual pairing by pigeons was reported by Whitman (1919:28). Mr. Herman Smith (personal communications) has succeeded in establishing unisexual pairs, male and female, by confining two birds of widely-separated ranks in relative aggressiveness. It is the posture and psychological state associated with dominance or subordination which trigger the sexual responses.

Individuals ranking high in a social hierarchy have a precedence in certain activities, such as feeding, and among males, mating rights may be included, as was found in chicken (Guhl, Collias, and Allee, 1945; Guhl and Warren, 1946). When the female pigeons were tested in the flight cage with territorial males, similar results were indicated. However, among the pigeons territoriality increased the opportunities for a relatively unaggressive male to pair if a female tended to remain in his area. Under the highly competitive conditons in this test (a sex ratio of 11 males to one female) the most aggressive males violated territory boundaries most often. This test did show that male pigeons may under certain conditions have pairing rights irrespective of territory.

One advantage of territorialism among pigeons was demonstrated when 12 females were introduced into the flight cage with 11 males. With the sex ratio nearly one to one all the males formed pair-bonds, and highly-aggressive males gave indications of some disadvantages. These males had difficulty in concentrating their attention on a particular female. With the females being distributed about the cage the opportunities for each male to pair were increased. Among free pigeons this competition would be less strenuous since it would be unlikely that many males or females would be in the readiness phase of the reproductive cycle at the same time, and defended areas may have wider distribution. Territory violations might be fewer than in this experiment.

The Common Pigeon is a suitable laboratory animal as it adjusts readily to confinement and handling. Being somewhat ambisexual in behavior, it could serve as an experimental animal in certain studies of the endocrine, social and sexual interrelationships. With refinement of the technique presented here on the measurement of aggressiveness, some of the difficulties experienced in the past (Bennett, 1939, 1940) could be surmounted.

Summary

1. The relative aggressiveness of Common Pigeons was measured by means of paired encounters in a combat cage or neutral area.

2. Pairing behavior was facilitated through submissive behavior by the female.

3. The most aggressive males had precedence in pairing if under extreme competition with other males and when confined in flight cage.

4. Territorialism made it possible for all the males, irrespective of levels of aggressiveness or dominance, to establish pair-bonds, when the number of individuals of each sex was nearly equal.

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NESTING BEHAVIOR OF THE WOOD THRUSH

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FROM 1942 to 1954 I watched, sketchily to intensively as my circumstances permitted, 37 nestings of the Wood Thrush (*Hylocichla mustelina*) in suburban Baltimore, Maryland, concentrating on the early stages that I had missed in a previous study (Brackbill, 1943). Many of the birds studied were color-banded.

Arrival and Pairing

Arrival of breeding males.—Breeding males sometimes were and sometimes were not the first Wood Thrushes in their territories in spring. My best example was a male that I color-banded in 1942 on April 29, the day of the species' arrival; in 1943 Wood Thrushes arrived April 28, but this male not until May 8, when he had to oust another male from his old territory; in 1944 the species arrived April 26 and the marked male April 27.

Returns.—Four of 10 color-banded breeding males returned, three in the year following their banding, and one in each of the two years following; three of these birds may have returned oftener, but at that point I moved from their neighborhood. Of 10 color-banded breeding females, one returned, the year after its banding. From 26 color-banded nestlings I obtained no returns.

Time of pairing.—Two males obtained mates one and three days, respectively, after their own arrival. Weaver (1949:103, 104) reported three males obtaining mates two, three and six days after arrival. I have never seen the manner of pair formation.

Retention of mates.—Both members of three pairs of multiple-brooded birds were color-banded; these pairs stayed together throughout the season. In none of five possible cases did both members of a color-banded pair return, and so there were no rematings from year to year.

The Nest

Tolerance for human habitation.—The increasing neighborliness of the Wood Thrush has been noted by Weaver (1939:16) at Ithaca, New York, Todd (1940:441) in western Pennsylvania, and Griscom (1945:59) in the New York City and Boston areas. Such a change in behavior of Wood Thrushes has occurred in the Maryland region, too, in the first quarter of the century. Writing of the Baltimore area, Resler (1891:106) said this bird "appears to be not so well known as the majority of our other songsters, in consequence of being more solitary and shy." Maynard (1902:44) said that in the District of Columbia area it is "an inhabitant of most woods about Washington," but Cooke (1929:65) stated that "they now nest freely about

lawns in the suburbs as well as in the woods." And from 1942 through 1954 they have been common in the wooded residential parts of Baltimore, with a pair often to be found every few blocks, or even every block for a little distance.

Twenty-five of my nests were on the grounds of occupied houses, three on vacant lots between houses, three in trees growing at curbs, two in the edges of a park opposite houses, and only three in wild land and one appreciably inside a park. As for proximity to dwellings, two nests were in bushes against the walls of houses, one was two yards from the back of a house and only a little farther from the steps, and five were in bushes marking property lines, with houses only three and four yards away on two sides.

Nest-site selection—A few observations show that the male Wood Thrush can influence the choice of a nest-site, but they suggest that the choice is actually made by the female—the nest-builder. The male, by means of calls or song, sometimes brings potential sites to his mate's attention, and he may even initiate building. However, the female may or may not adopt sites thus indicated, and so it seems that she must be regarded as the true site-selector.

Observations of a pair in 1949 were most illuminating; these birds were not banded. One evening I found the male singing at a horizontal fork low in a tree. Soon the female flew beside him and in some seconds he left, and then the female began a period of "nest molding" at the fork. While she was still there, the male flew well up into a different tree with a piece of white paper. The female shortly left the fork and I lost sight of both birds, but a little later one or the other of them took paper into a third tree—to a point at which I could see no other material—and it was there that building continued, the builder being the female all of five times that I could make an identification (the male was singing elsewhere).

In 1943 the first nest of a color-banded male was on the same branch as his first nest of 1942, and on almost the same spot, although he had different mates in the two years. Since his territory contained a variety of suitable nest-sites (proved by the fact that he and three mates also used four others there during three years that he was under observation), necessity did not cause this duplication, and it is inconceivable that chance did. Certainly this male influenced his 1943 mate to build at the old site. Two incidents suggest how this was accomplished. An hour and a quarter after I first found him with his 1943 mate I saw him at the old site, giving bursts of very loud *quit* calls. The next day the nest was begun there. The day after that, I thought, but in dim light could not be sure, that the banded male made the second building trip of the day. Thus it may be that the male's calls attracted the female's attention to the spot, and it is also possible that the male carried a little material during the earliest building—although from then on the working bird whenever identified (10 out of 14 trips) was the female.

In 1944 I made a somewhat similar observation on this same male. On the evening of May 4, the day he obtained a mate, I came upon him in an oak that in the previous two years had been one of his principal singing trees giving extremely muffled and unmusical song trills and calls; his mate was on the ground about 13 yards away. On May 9 I first saw the female tentatively pick up nest material; on May 13 I found the nearly-completed nest in the oak mentioned.

Weaver (1949:103) describes a female testing a site in much the manner

of my 1949 female, and (1949:106) reports that "in one case a pair built in the identical spot it had used the year before."

Height.—I believe the 37 nests I located comprised all but two of the entire number built in my study areas. In this suburban environment the height range, 4 to 35 feet, was typical of that generally reported for the Wood Thrush, but there was a much greater proportion of moderately high nests than Preston and Norris (1947:256) found in natural woodland. Almost half of my suburban nests were at 13 to 22 feet, whereas two-thirds of those in natural woodland were at 5 to 10 feet. This seems attributable to the fact that trees of sapling size are uncommon in residential areas; from the upper branches of shrubs to the lower branches of large trees there is a stratum in which few building sites are available. Of my nests, 12 were in bushes, 6 in saplings, 19 in large trees.

Placement, materials.—I have little to add to Weaver's account (1949:105–106) of nest sites and materials, except as regards the statement that "the nest is usually fixed in a fork . . . but some were found saddled on horizontal branches."

In my experience, nests are often set on the base of a horizontal fork, a spot that provides broader support than a single stem. Similarly, nests on straight horizontal branches are generally placed at a spot where one or more twigs grow out, or where the branch is crossed by another stem of the bush or tree or by a vine. The thickness of branches at nest-sites has varied from ½ inch to 3 inches. I have never seen a nest set in a two-pronged vertical fork, but have found some inside multiple forks, or "baskets," of upward-growing stems. The branch chosen for a tree nest is usually the lowest on its side of the tree, if not the lowest on the tree; of 15 nests on which I have notes, 9 were on the lowest branch on at least their side, and three on the next-to-lowest; the others were as high as the fourth tier of branches. Tree nests as a rule have been one-third to three-fourths of the way—three to 11 feet—out branches; one exception, in a sapling, was built against the main stem, its base resting on thin twigs that formed a slight crotch. Like Weaver (1939:16), I have never found a nest in a conifer, though many were available and one was used as a song perch. Neither have I ever found a nest in the thorny bushes—rose, barberry, pyracantha—that are commonly used by some species in the same suburban areas. Nests in other bushes may be either in the heavily-foliaged crowns or among the lower, leafless stems.

Concealment, shade.—With both tree and bush nests, the degree of concealment varied greatly. In trees, the lateral twigs that gave secondary support occasionally bore leaves that almost entirely hid the nests. More often, the nests' similarity in color to their supporting branches, and their tendency to melt into the mottled background of light and shade created by foliage, made them hard to locate. Nests in the crowns of bushes were sometimes

practically invisible, but those down among scantily leaved stems were fairly conspicuous.

The customary use of sites low in trees insured shade from the foliage above. Thick crown foliage or overhanging trees shaded all but one of the nests in saplings, too—that one was considerably exposed to the afternoon sun but was completely successful. The bushes used for nesting were with one exception well shaded by trees.

Size.—Not counting the materials that occasionally hung down as much as 14 inches below the base proper, seven nests (six bush, one tree) had outside heights of 2 to 5¾ inches and widths of 4 to 5½ inches. One was 4½ inches wide at the base but only 4 at the rim. One built on a slanting branch was made level by being 3¼ inches deep on the lower side and only 2 inches deep on the upper side.

The inside depths of the seven nests ranged from 1¼ to, usually, 2 inches, and the inside width from 2¾ to 3¼, or occasionally, 3⅜. Two nests were not quite round: 3 by 3¼ inches and 3¼ by 3½ inches in inside diameters. One nest measured only after its two young had left was 4 by 4¼ inches, indicating that use had widened it about an inch.

Successive nests of the same birds.—I have already (1950:8) shown that successive nests of the same pair of Wood Thrushes may be at heights as similar as 17 and 13 feet or as dissimilar as 18 and 8 feet, and that they may be dissimilar in their placement. An additional observation is: a color-banded pair of birds in one year had successive nests 9 feet up in a lilac, set in a "basket" of four stems; 6 feet 6 inches up in a silky cornel, set on a fork that slanted upward at 45 degrees, with another branch supporting its lower side; 5 feet 10 inches up in the top of an unidentified bush, set on a horizontal fork, from one arm of which two twigs grew out.

With five out of six pairs of marked birds, successive nests have been progressively lower; the sixth pair nested at 7 feet 3 inches, 13 feet 9 inches, 10 feet 9 inches.

I have never seen a nest used twice in the same year, and have never seen one survive weathering from one year to the next.

Sex of the builder.—Observations at 12 nests, ranging up to 9½ and 19 hours' watching of color-banded birds, showed building to be a female activity. Aside from the uncertain 1943 occasion, and that of 1949 during nest-site selection, both described above, I only three times saw males work, and those birds did not add material but merely molded during absences of their mates.

On June 27, 1948, the third nest of a pair was being lined. When the female left on what became a 20-minute absence, the male flew to the nest-rim. He occasionally pecked in the nest, then after 11 minutes entered it and began molding, just like a female but less vigorously. He worked sporadically until just before his mate returned, his halts being made to mark the doings of other birds in the neighborhood, and once to sing for half a minute in response to a neighboring thrush.

On May 15, 1954, the first day of work on a first nest, a male twice, during absences of his mate, went to the nest without material and worked in it, once for two minutes

and once intermittently for nine, both times leaving only when his mate returned. He, too, worked just like a female, in molding, in moving material from one spot to another, and in lapping straws from the outside up over the rim into the inside.

Building hours.—I saw building done as early as 5:00 a.m., E.S.T. (10 minutes after sunrise), as late as 7:32 p.m. (two minutes after sunset), and at all hours between except for the period from 3:00 to 4:50 p.m.; however, usually only on the days of intensive building was there work in the afternoon. Nests are often begun in the evening. On the second and third days, which are generally the days of most intensive work, building may be done in the evening as well as the morning and early afternoon. I once saw work done on the evening of a fourth day. Later than that, when the nest is generally getting mere touches, these seem to be given it only in the early morning.

Time required.—The time taken to build five nests was determined: two first-brood nests, five days; one first-brood and one second-brood nest, six days; one first-brood nest, seven days. In each case, only slight touches were given on the mornings of the last two (once three) days. I did not obtain precise data on successive nests of any bird.

Source of materials.—Materials at times were gathered as much as 70 and 85 yards from the nest-site, but I believe most were obtained within 25 or 35 yards. Besides loose-lying materials, rooted grass—both dead and living—is pulled at and sometimes obtained.

Manner of building.—At no single nest was I able to watch building procedure throughout, but at one nest or another I saw all stages of work, and I saw most stages more than once. The following account is a composite.

Soft white paper, cellophane, string, or long stems of dead grass—usually some combination of those things—are first draped across the nest-site; they commonly hang down a number of inches below the branch. Dead grass, rootlets and dead leaves are then placed atop this; as she adds each billful the female squats on it and squirms about, packing it down.

When a substantial foundation has been achieved in that way, the nest wall is begun. Arriving with more material, the bird drops this in front of her or to one side, then reaches to the edge of the nest-mass and pulls some of the outer material upward and inward and tucks it into the bottom; this lapping-over may be done several times in succession. Then the bird "molds"—squats and, with wings, rump and tail all more or less raised, apparently presses forward with her breast while also using her feet behind her. Rises, turns a varying distance to one side or the other, perhaps does more lapping-over, and molds again. As many as 30 molds, taking the bird around in the nest for three full circles and occupying as much as six minutes, may be made on a single visit to the nest. In this way the material about the outside of the mass is gradually pushed and built upward and compacted into the nest wall. In the later stages of this work, lapping-over from the outside is sometimes omitted, but loose ends of material that project into the nest-cup are frequently tucked back into the wall.

Only one bird was watched while putting in the mud layer of her nest. She did this by means of typical molding, and sometimes held an appreciable amount of mud on her bill during a number of molds, apparently distributing it in the course of her work. The lining of rootlets is also worked into place by molding, but molding in which the

feet seem to be used much more than the breast. At the nest I was able to watch most lengthily, the number of molds made on one visit increased, as building progressed, to a maximum when mud was being used, then decreased somewhat as the nest was being lined.

Generally, the nest is really complete after three days' work. On two or three more mornings, however—as late as her first egg-laying day—the female may still give it a few touches. During this period, one bird sometimes added material, and sometimes went to the nest empty-billed, stood in it idly during the greater part of her visit, and only occasionally made an adjustment. Another bird, on the morning of her first laying day, sometimes seemed to take a bit of material from one spot and put it as much as 90 degrees farther around the rim; she also seemed occasionally to move something from the rim to the bottom of the nest, and she still sometimes lapped material slightly over the rim.

This is the same method of building that Herrick (1935:174–175) has recorded for the American Robin (*Turdus migratorius*).

Reversals of direction in molding.—Herrick noted (1935:174, 193–196) that when making a number of molds during the same working visit to its nest, a Robin normally keeps turning in the same direction—to its right, say—and then on its next visit makes its turns to the left, and so on alternately. However, if it makes an extreme number of molds during one visit, the direction of its turns may be reversed once or oftener in the course of that visit; the reversal is "related rather to the number of molds than to that of the visits."

At a nest at which I paid particular attention to this point, the Wood Thrush behaved similarly. During the first 185 minutes of one working day, for example, this bird made 42 visits to her nest. With L meaning left and R right, and spaces merely setting off the series of visits during which reversals were made with complete regularity, the direction of her turns throughout each visit was:

RLRLRLRL	LRLR	RLRLR	RLRLRLRLR	RLRLRL	LRLRLRL	LRL... (series
74	36	44	74	76	72	36 ... unfinished)

The figures below each series are the closely approximate number of molds made during that series. It may be noted that the second failure to reverse occurred after an interval of only one minute between trips; this suggests that the third series should be regarded as a continuation of the second, and if that is done it is apparent that a true failure to reverse occurred with great regularity after about every 75 molds. In contrast to that failure to reverse direction after a one-minute absence, the first two trips of the day show a reversal although 30 minutes elapsed between them; Herrick (1935:193) similarly records a reversal by a Robin after a 24-minute absence.

Rhythm.—When building intensively the working female showed an attentive-inattentive rhythm like that of incubation. Examples from three nests are:

Second nest of year, second day of work, 9:41–10:45 a.m.:

Attentive (minutes)	+ 17.5			1			14.5			
Inattentive (minutes)			11.5			8.5			11	

Third nest of year, same bird, third day of work, 9:28–11:08 a.m.:

Attentive			43.5			5				
Inattentive	+ 12.5			20			19 +			

First nest of year, third day of work, 5:10–8:15 a.m.:

Attentive	+ 5		1.5		12	14		83.5		6.5
Inattentive		30		6.5	6		10		7.5	2.5 +

During the last series of attentive periods listed, the number of building visits made to the nest was 1, 1, 6, 6, 25 and 3, respectively.

A building drive.— Once a long strip of crepe paper that a female was taking to her nest caught in the bush 2½ feet away. She tried to dislodge it and failed, but then instead of going for other material went on to the nest and worked just as if she had added something. I have seen a male House Wren (*Troglodytes aëdon*) act similarly. One that was carrying twigs into a nest-box often had difficulty maneuvering them into the hole, and five times I saw him knock them out of his bill. Once this happened as soon as he alighted at the box, and that time he went to the ground and recovered the twig, but the other four times it happened only after he had been struggling with the twig for some time, and on all of those occasions he then went into the box empty-billed and stayed as long as if he had added material. It appears that, once started on a building action, both of these birds had to carry it through, even though the original motivation no longer existed.

Male's activities during building.—At seven nests, of five pairs of birds, I obtained more than casual observations on the male's activities during the building period. Different birds acted somewhat differently, but it is possible to summarize as follows: the male sings, but usually not very much, throughout this period; he defends the territory, but very imperfectly; he begins to stand guard at or near the nest during some of the female's inattentive periods—two males entered the nest and molded, as related above; during the later stages of work he sometimes accompanies the female to and from the nest and stays nearby while she builds; at this time he also engages in sexual flights with her; and he feeds the young of the preceding brood, if there are any.

Copulation

I did not see copulation, but during the building and laying periods at several nests saw sexual flights and other possibly stimulatory acts, and saw one male attempt copulation and fail—apparently because the female, which had begun to incubate, had passed that stage of her sexual cycle.

Early on the morning of May 9, 1943, only a few hours after the female's arrival in one territory, I found her with the already-color-banded male on the lawn. Twice within three minutes she toyed with pieces of cloth and cellophane, and between times once ran at the male and seemed to peck him. Nothing further occurred during the few minutes more the birds stayed there. Nest-building began the next day about 12 yards from that spot, and the first egg was laid May 14. A similar incident occurred on May 28, 1949, five days after a storm had destroyed the nest and eggs of a color-banded pair. At noon, while the birds were feeding on a lawn, the female once ran at the male and apparently pecked him; some squeaky calls were given by

one bird or the other during the incident. Again, nothing further occurred. I think the first egg of a new set was laid the next day. Both of these incidents looked like attacks, but as copulation must have been occurring at the time, or about to occur, perhaps they were stimulatory.

Sexual flights were seen at various nests, as early as the third day of building and as late as early morning on the second of three laying days, when incubation had begun. The birds flew at a moderate speed over winding courses, often only three or four feet above the ground. Eight out of nine flights were made in silence; during the other, long *eeee*'s were frequently given, but I could not tell whether by one bird or both. Some males were singing just before the flights began; song was sometimes resumed afterward. The flights were seen oftenest in the early morning, but also in the evening and once around noon. One pair of birds made two within four minutes; another pair made four within 45 minutes. One female made a building trip to the nest between two flights that were 11 minutes apart. Weaver (1949:104–105) describes similar flights.

On June 2, 1943, the first egg was laid in the nest of a color-banded male and an unbanded female. At 5:45 a.m. on June 3 the female was incubating and the male singing nearby. After 20 minutes the female flew about 50 yards away, and almost at once the male disappeared. Some minutes later, from my place near the nest, I saw two thrushes flitting about perhaps 10 feet up in a tree in the area to which the female had gone; there were wing-flutterings and apparent attempts at mounting, then the birds went out of sight on a sexual flight. Shortly after this the pair alighted 25 feet up in a tree near the nest, and there, with neck stretched high and crest raised, the male began persistently running along a branch at his mate and bumping her on the side or shoulder with his breast; often he fluttered his wings a trifle. Sometimes, too, he flew hoveringly at her as if to mount, and once he did drop his feet to her back and then opened one wing horizontally and fluttered it briefly; the female, however, moved from under him. After a minute the birds went into a tree still nearer the nest; there the male continued his actions, but now sometimes when he approached the female she pecked at him and drove him back. Two and a half minutes after these performances had begun, the birds again flew out of sight, and during the few minutes more that I could watch they did not return. According to Howard (1929:52) this was typical behavior for a male that is still sexually eager and a female whose copulation period had just been ended by the beginning of incubation. The attempts at copulation in trees contrast with Weaver's belief (1939:21) that she once saw it take place in the air, and with her statement that A. A. Allen believes it normally takes place on the ground.

The Eggs

Interval between building and laying.—At 10 nests, the first egg was laid from one to three days after building had been essentially completed. Three of these nests were among those seen to be given slight touches on the later mornings, as related under "Manner of building." Because there was indication of this at a fourth nest also, and because such working trips were so few that only prolonged watching disclosed them, I believe this behavior probably is the rule.

Laying rate.—Eggs are laid one a day on successive days.

Clutch size.—Sixteen clutches observed as laid or (two of them) found during the first few days of incubation ranged from 1 to 5, with 3 and 4 most common. The division was: 1 c/1; 2 c/2; 6 c/3; 6 c/4; 1 c/5.

Clutches tended strongly to be largest at the beginning of the season. The c/5 was a first clutch. Five of the c/4's were first clutches and one a third clutch. Two of the c/3's were first clutches, three were known second clutches, and the other was indicated by its date to be a second clutch. Both c/2's were second clutches, and the c/1 a third clutch.

Clutches smaller than 3 eggs all followed some disturbance of the breeding cycle. One c/2 was laid after a storm destroyed the first nest during incubation. The other c/2 followed a nesting in which only a Brown-headed Cowbird (*Molothrus ater*) was raised, and the c/1 was a third laying of this same female after a storm destroyed her second nest and eggs.

Successive clutches of same females.—Successive sets of three color-banded females showed no fixed relationship in size. One bird whose nestings were undisturbed laid clutches of 3 and 3; another, 4 and 3. One whose first nesting was unsuccessful laid three clutches of 4, 2 and 4; in the following year this female's first clutch numbered 5—this is the only bird on which I have data for more than one year.

Laying dates.—The earliest observed laying date was May 12; the latest, July 6. Eight first clutches were laid in the period, May 12 to 21. Three second clutches of birds that had undisturbed first nestings were laid June 16 to 26. Two third clutches of birds that had had one previous failure were laid July 1 to 6. Cooke (1929:65) reports eggs as early as May 1 in the Washington, D.C., region, and Kirkwood (1895:370) gives a late date of July 28 for Maryland.

Laying hour; effect of temperature.—Data on 18 eggs, representing nine nests, show that laying is usually done between 9:00 a.m. and noon, E.S.T., but sometimes not until early afternoon. At least 12 of the eggs were laid after 9:00 a.m., and at least 11 were laid before 12:15 p.m. The earliest-found egg was laid between 7:55 and 9:34 a.m., and the next-earliest between 9:11 and 10:14 a.m. The latest was laid between 1:30 and 4:48 p.m.; two

others were laid between 11:42 a.m. and 1:35 p.m., and 12:57 and 2:20 p.m. Weaver (1949:107) reported two eggs laid at about 10:30 a.m.

It appears that laying is done earlier on cool days than on warm ones. All of nine eggs known to have been laid before noon (by six different birds) were laid on days when the temperature at 6:00 a.m. was 52 to 58° F.; the mean temperatures for those days ranged from 11° below normal to 4° above normal. All three of the eggs that were laid after 11:42 a.m. (by two different birds) were laid on days when the temperature at 6:00 a.m. was 70° and 71°; the means for those days ranged from 6° to 16° above normal. The earliest-found egg was laid on a day that was 4° below normal, and the latest-laid egg on a day that was 6° above normal. (The temperatures given are the official ones for Baltimore city, not those in the nesting territories, and so are relative rather than exact.)

Fledging-to-egg and egg-replacement times.—At four second-brood nests the first eggs were laid 9, 9, 11 and 12 days, respectively, after the young had left the previous nests. Weaver (1939:22) reported one interval of "16 days," but the dates given show 17, and her statements there and those reported later (1949:112) conflict.

Laying was resumed more quickly—on the seventh day, and not later than the eighth day—after the destruction of two nests by storms on the third and eighth days of incubation, respectively. The bird that had begun her second clutch on the eleventh day after fledging her first brood was the one that now laid in a third nest on the seventh day.

Nice (1937:111, 133) found that with the Song Sparrow (*Melospiza melodia*) the fledging-to-egg interval is longer and more variable than the egg-replacement time after destruction of a nest. Blanchard (1941:34) also found this true with the White-crowned Sparrow (*Zonotrichia leucophrys*), and Walkinshaw (1945:12–13) with the Field Sparrow (*Spizella pusilla*). Lack (1953:201), however, reports great variation under both circumstances with the British Robin (*Erithacus rubecula*).

Incubation

Sex.—Observations at 17 nests, ranging from one to 68 identifications of the sitting bird—more than 10 identifications were made at each of nine nests—confirmed my previous finding (1943:75) that the female alone incubates. Weaver (1949:108) also found this to be true.

Brood patch.—The brood patch begins to develop within the week before laying starts. Three females had the abdomen still feathered when banded six, seven, and six to eight days before they laid their first eggs; at least two of these birds had begun their nests at the time they were trapped. A fourth female, trapped when her nest was near completion, had only a few downy feathers on the abdomen; I do not know when she began to lay.

Time and manner of start.—Observations at 14 nests show that daytime incubation usually begins on the second laying day, but sometimes on the first and sometimes as late as the fourth. It most often begins on the penultimate laying day, but may begin as early as the first of four. Night roosting on the nest sometimes begins with the first egg, sometimes with the second. I can demonstrate no clear difference in behavior as between first and second broods; two of three nests at which daytime sittings began with the first egg were second-brood nests, but the two nests at which roosting began with the first egg were first-brood nests.

Close observations on the start of daytime incubation were made at 10 nests. At three there were some sittings from the first laying day, at five from the second laying day (at three of these, at least, beginning some hours before the second egg was actually laid), and at one each from the third and fourth laying days. At five out of the 10 nests the sittings began on the day of the penultimate egg, but two birds began with the first of four eggs, and three on the second of four laying days. Except at an eleventh nest, in which only one egg was laid, no bird completed her clutch before beginning to sit.

Another bird, which laid three eggs, was already incubating early on the morning of the second laying day, when her nest was found. At a nest in which a Cowbird egg, and then a thrush egg, were laid on successive days, incubation began early on the morning of the second day, before the thrush laid. And at a nest in which two thrush eggs were laid, and then a Cowbird's, there was some incubation from at least the second of the three days.

The way in which incubating behavior develops can be illustrated through one female and her two nests. My observations were fullest at the first nest, in which four eggs were laid. With the laying of the first egg the bird began to spend brief periods, very occasionally, standing on the rim of the nest. With the laying of the second egg, periods of such attentiveness became much more frequent, and finally changed into some covering of the eggs. With the laying of the third egg incubation became typical and steady. At the second nest, in which three eggs were laid, the same behavior apparently developed one day faster, for during an hour's watching early on the morning of the second laying day I saw not only one period of simple attendance on the nest-rim but part of an appreciable sitting.

Amount and rhythm.—Some figures on the attentiveness of females during incubation of full clutches (*i.e.*, laying and hatching periods excluded) are given in Table 1. For the sake of completeness two earlier ones (Brackbill, 1943:75) are repeated on the first two lines of the table. The females usually ended their sittings of their own accord, but sometimes ended them (and sometimes did not) when their mates came near the nest or began singing in the vicinity.

Hatching hour.—Hatching may occur during either the day or the night. Data were obtained on 24 eggs in 11 nests, as follows: 18 hatched during daylight—four of these between 5:00 and 7:00 a.m., E.S.T., one between 9:30 a.m. and 1:40 p.m., one at 3:35 p.m., one between 5:00 and 6:00 p.m., the other 11 at unknown hours; six hatched during darkness.

The 24 eggs included eight final eggs of clutches; of these, four hatched

TABLE 1

ATTENTIVENESS OF INCUBATING FEMALE WOOD THRUSHES

	Hours Watched	Eggs Covered	Attentive Periods No. Seen	Attentive Periods Range in Min.	Attentive Periods Average	Inattentive Periods No. Seen	Inattentive Periods Range in Min.	Inattentive Periods Average
First-brood nest	15¾	78.0%	11	11–47	31.0	22	6–16	8.5
Second brood, same bird	17	80.3	12	7–58	27.0	18	1–12	6.1
First-brood nest	5	88.0	5	11–42	25.0	8	6–13	8.0
Second brood, same bird	4	60.0*	1	45		6	2– 9	5.0
First-brood nest	9¼	69.2	23	2–28	13.6	25	2–23	6.1
Renesting after failure	7½	75.6	8	17–37	26.0	13	4–11	6.0
First-brood nest	29	71.2	37	6–49**	24.4	47	4–21	9.8

*Time spent at the nest without covering the eggs would raise total attentiveness to 94 per cent.

**Another attentive period, on a hot day (78° to 82°F.) was still unfinished after 80 minutes. However, during it the bird frequently stood up and picked in the nest for periods of one to five minutes; the eggs were covered for only 45 of the 80 minutes. With this one exception, incidentally, all of that bird's attentive periods during incubation were much shorter than the sittings during which she laid her eggs; those were:

Egg 1 laid sometime between	9:11–10:14 a.m.;	sitting less than 63 minutes
Egg 2 sitting	9:55–11:00 a.m.	65 minutes
Egg 3 sitting	9:32–10:55 a.m.	83 minutes
Egg 4 sitting	10:13–11:40 a.m.	87 minutes

during daylight, three at unknown hours between 6:00 p.m. and 7:00 a.m., and one definitely during darkness.

At one nest I flushed a bird at 4:26 a.m., 17 minutes before sunrise, and found an egg hatched, the shell still present and both it and the nestling dry, indicating that this night hatching had occurred sometime earlier but the parent was waiting until a normal time to leave the nest.

Hatching order.—All of the eggs in four marked sets, and at least the final two eggs of four more sets, hatched in the order of laying. In one of the latter sets, however, Egg No. 2 hatched at least half an hour before Egg 1; there had been some incubation at this nest from the second laying day.

Spread of hatching.—Precise observations at one nest showed that hatching was spread over 39 hours. At five other nests I learned only that the spreads were greater than 25, 27½, 31¼, 34 and 39 hours, respectively.

Egg shell disposal.—The female carried away both halves of one shell, but not until an hour after the nestling had freed itself from at least one half; in the meanwhile the female had made three more sittings, and both parents had made or attempted to make some feedings. I had once before seen a shell carried away (1943:76), and Ivor (1952:286) has reported this method of disposal.

Incubation period.—Incubation period here means the time between the

laying and hatching of the last egg of a set. The time of hatching was counted as that when a bird severed its shell so that one half fell away, when the bird was found still within one half of the shell, or when it was found with down wet and part or all of the shell still in the nest.

Observations at eight nests show the incubation period to be about 12¾ days. My closest timing was of a marked egg that took 12 days, 19 hours, 39 minutes ± 44 minutes to hatch. Another took 12 days, 21 hours, 11 minutes ± 6 hours 32 minutes. All of six other eggs (five of them marked) took more than 12 full days to hatch; at least two of the six took more than 12 days, 12 hours. The maximum possible time for one egg was 12 days, 18 hours, 5 minutes, and for another 12 days, 20 hours, 55 minutes. Weaver (1949:108) gives 13 days for marked final eggs in two nests at Ithaca.

Overtime incubation.—An egg that was the only one laid in one nest, and that never hatched, was incubated for 25 days—from July 1, the laying day, until sometime on July 26.

Female's incubating behavior.—Most females sat very patiently, at least during the early days of incubation, merely rising occasionally to turn the eggs with their bills, or to change their position somewhat; sometimes they squirmed around to face a different direction without rising perceptibly. One bird whose rises and resettlings were recorded through 13 sittings showed no regular alternation of direction in her turns, either within or between sittings. Now and then the birds may preen, or may doze a bit. One once left her eggs for a moment to pick an insect off a nearby branch. In the later stages of incubation, especially, birds commonly rise frequently and use their bill in the nest with a motion like the drumming of woodpeckers; although this suggests a probing for mites, my fingers held briefly in the nests on these days have not always produced any.

Observations at two nests when the official temperature was 76° F. and higher showed much attentive time being spent standing above the eggs instead of covering them. One female, watched for 71 minutes when the temperature was 76 to 78° F., spent 25¾ of 62 attentive minutes standing above the eggs. Watched for 104 minutes when the temperature was 85 to 89°, this bird spent 54½ of 101 attentive minutes so. The dates were four and one days, respectively, before hatching began.

Another female, watched for 123 minutes while the temperature was 79°, 78°, 82° and the sun was continuously splashing her or the side of her nest, spent 40 of 113 attentive minutes standing above the eggs, and, while sitting, occasionally held her bill open. On the other hand, 115 minutes of watching two days earlier, when the temperature was 82° to 78°, showed no such actions. These dates were five and seven days before hatching began. Like the brooding female of my earlier paper (1943:77) this bird often stood on the nest-rim, but not on the sunward side.

Male's activities during incubation.—Observations of appreciable length at five more nests confirmed my earlier findings (1943:75–76). During their mates' attentive periods, males generally sang considerably, often from nearby perches that enabled them to defend the immediate area of the nest; they foraged, sometimes far from the nest; and with varying frequency they paid brief visits to the nest-bush or tree, sometimes going within a few inches of the nest; these visits occasionally led the females to end a sitting.

During their mates' inattentive periods the males almost always stood guard over the nest; at second nests they did this with much regularity even though they still had first-brood fledglings in their care. The guard perch was often the rim of the nest, but sometimes was elsewhere in the nest-bush or in some nearby tree. It was not uncommon for some singing to be done during this guarding, even from the nest-rim.

Nestling Period

How male learns of hatching.—I was present during hatching of the first egg at only one nest; there the male learned of hatching by seeing the nestling and seeing his mate feed it. Twenty minutes later he also began making feedings.

I began watching this nest at 2:42 p.m.; the female was sitting. At 3:35 she left and I found the first nestling out of one-half of its shell. There had been no sign of the male so far, and he did not come now to guard the nest. At 3:43 the female returned and went on the nest without making a feeding. At 3:48 the male arrived at the nest-rim and the female left; the male had no food, and merely stood looking into the nest until at 3:52 the female returned; he then moved aside but stayed close while she seemed to make a feeding, after which he left. At 4:09 he returned with food and gave it to the nestling.

Ivor (1952:286) believed that at a nest he watched, the male learned of the hatching in some other way.

Feedings.—Both parents feed the nestlings.

At one nest the first bird to hatch was first fed by the female, perhaps only 17 minutes after it hatched, and was first fed by the male 17 minutes after that, as described just above. During its first hour this nestling was fed at least three times, and probably five, then it once refused food.

One pair of observations showed the feeding day to be 15 hours (4:31 a.m., E.S.T., sky partly cloudy, to 7:35 p.m., sky clear). The first feeding was made 10 minutes before sunrise and the last seven minutes after sunset. On a clear morning the first feeding at this nest was made 19 minutes before sunrise.

Once while a male was standing on the nest-rim after making a feeding and eating a dropping, the two newly-hatched young shortly resumed gaping. After they had gaped for some time the male thrust his empty bill into each mouth a few times. Schantz (1939:164) has reported such behavior by American Robins.

Nest sanitation.—Although at two previous nests I had seen feces carried away a few times (1943:79) and I later saw this at two more nests, during

13 and 18 hours of watching feedings at two others all excreta were eaten, even on nest-leaving day. As I had found before, when the female remained at the nest through feedings by the male he did not wait for excreta to appear.

Brooding.—Observations at seven nests showed this to be done by the female alone, and at three nests I again found it to be done throughout the young birds' nest life (*cf.* 1943:77).

At one nest, brooding was done for 45.6 per cent of 6½ hours that I watched. There was no decrease in amount as the young grew, but there was some inverse correlation with temperature.

The male, during the nestling period, not only helps with feeding and sanitation, but continues to guard at or near the nest during many of the female's inattentive periods. At the nest I watched most closely, he regularly guarded while the young were small, and for decreasing portions of the female's absences, and at varying distances from the nest, when the young were large; occasionally he did some singing while on guard.

Nestling period.—Ten young birds left the nest at the age of about 12 to 14 days. Two left at about 12 days, two at about 12 and 13, one at 13, two at 13 or 14, and three had been in the nest 12 and 13 days when I caused premature departures.

Fledgling Period

Feedings.—Both parents feed the fledglings. The females of two pairs helped to feed their first broods even while building their second nests; they made feedings at least as late as the second day before, and the day before, they resumed laying. When the young of single or final broods are all out of the nest each parent cares only for certain ones, and there may be a very similar division of the care of first broods; my observations on this point, with color-banded adults (one exception) and young are:

First broods: With one brood of three, the male alone was seen to feed two fledglings (12 and five observations) but the female helped to feed the third (two feedings by her, five by male seen) through the second day before she again began laying, after which the male alone was seen to feed that bird too (six more observations). This is an elaboration of my statement (1943:79).

With a brood of four, I saw only one feeding of each fledgling, but the male fed two of the birds and the female the other two.

Single or final broods: I had already seen the care of one second brood divided between the parents (1943:79), and Weaver (1949:112) has reported this for an unspecified brood. Two further sets of observations on single-brooded pairs are:

An already-color-banded fledgling that I caught and held for half an hour in an effort to decoy the unbanded female was attended only by the male; its most persistent calls during his absences never brought the female. Later I again briefly watched that fledgling and again the male was the parent in attendance. I saw another of the brood cared for by the unbanded female; once the male drove off a Robin that alighted near this fledgling, but it ignored the fledgling itself.

At another nest I took particular pains with this point. When two of the three young

had left the nest the male fed both; I do not know whether the female fed either. The male also helped the female feed the final nestling during at least part of its last day in the nest. This third bird vanished immediately upon leaving the nest. The parents then divided the care of the other two; I watched feedings on all of 12 days that the young remained in the territory, and saw the male feed one of them 85 times and the female feed the other 28 times. On the way to his bird with food the male once hopped close past the female's but ignored it.

Period of dependency and stay in natal territory.—One first-brood fledgling was partly independent by the age of 21 or 22 days, and two final-brood fledglings by 23 to 25 days. Three first-brood fledglings were last seen when about 22 to 24 days old, and four single- or final-brood fledglings when about 21 to 27 days old, in contrast to the 28 to 32-day ages I previously observed (1943:80–81). The two single-brood young that I watched most closely developed self-sufficiency as follows:

One first seen to peck at ground at age 17 or 18 days, definitely picking up inanimate things at 18 or 19, apparently eating at 24 or 25, last seen to be fed by parent and last seen in territory at 26 or 27 days.

Other first seen to peck at ground at age 19 or 20 days, apparently eating at 23 or 24, last seen to be fed at 24 or 25, last seen in territory at 25 or 26 days.

Number of Broods; Nesting Success

Full-season observation of nine pairs in which one or both birds were color-banded showed two broods to be the rule. Three pairs raised two broods and two more pairs had unsuccessful second nestings. Only two pairs disappeared after successful first nestings, though two other pairs disappeared after unsuccessful ones.

Seventeen out of 26 nests (65 per cent) in which eggs were laid produced young; at least nine of the 26 (34 per cent), and possibly 11, were completely successful. Nine nests (34 per cent) were total failures. Two additional nests were deserted before being completed. Of the nine nests that were total failures, three were destroyed by storms and two by unknown predators, three were deserted—one after a Brown-headed Cowbird parasitized it, one after an egg disappeared, and one for an unknown reason—and at one the single egg failed to hatch.

Of 44 eggs laid in 15 nests, 39 hatched (89 per cent), and 35 young were raised (80 per cent of the eggs, 90 per cent of the hatch).

Song

On the ground.— I have seen males sing on the ground eight times while foraging. One date was in April, five in May, one in June and one in July. The song has usually been intermittent but of good quality. The stage of the breeding cycle was: day after arrival, bird unmated, 1; mate building, 2; mate laying, 1; eggs hatching, 2; unknown, 2.

In flight.—Four times in June and July I have seen birds sing in flight—just one to a few phrases. One bird was pursuing or pursued by another Wood Thrush, one may have been trying to draw a fledgling Cowbird farther away from me; the other two were undisturbed, as far as I could tell.

Atypical Song.—Twice I have heard atypical song. On a May 11 one bird's phrases sounded, at a little distance, like a succession of *weet tyer's*; however, heard from very close by they had a fair vibrancy and some phrases were more typical. On a July 8 a bird had in its song some whistled, rather rapid *too-wee too-wee's*.

Another singing female?—Since I have seen one female that did much singing (Brackbill, 1948) and another that gave some single song-like notes (1943:82), it seems worth noting that in 1949 I suspected still another female of doing some singing fairly similar to that of the first bird referred to here, but only rarely instead of frequently. The days on which I heard such song were May 21, the sixth day of full-clutch incubation; May 24, the day following desertion of the storm-damaged nest, and June 5, the fourth day of full-clutch incubation at a new nest. I never succeeded in locating the bird that was giving the notes I heard; however, on May 22 I saw this female give, from the nest, two loud, raspy *tseee* notes that in quality were nearer to the suspected songs than to any other Wood Thrush utterances I have ever heard.

Cowbird Parasitism

Brown-headed Cowbirds parasitized three of the 37 nests, laying one egg in each, and in each case it appeared that this inhibited the laying of the Wood Thrush.

Nest 1: May 11, nest seems complete. May 12, inspections at 6:35 a.m. and 5:43 p.m. show no egg. May 13, a Cowbird egg present at 6:04 a.m., and only that marked egg present at 5:40 p.m. May 14, at 8:05 a.m. the thrush on the nest but only the Cowbird egg present; between 9:35 and 10:17 a.m. the thrush laid an egg. The thrush incubated those two marked eggs through the evening of May 17, then abandoned the nest.

Nest 2: May 16, nest with one thrush egg found; I marked the egg. May 17, second thrush egg laid and marked. May 18, Cowbird egg laid and marked; steady incubation was under way by this morning, my first opportunity to watch. No further eggs appeared. The first thrush egg hatched the night of May 28–29, the Cowbird egg on May 29, and the second thrush egg on May 30. The Cowbird disappeared when four days old; both thrushes were raised.

Nest 3: May 19, nest with one thrush egg and one Cowbird egg found. The thrush egg did not hatch. The Cowbird hatched May 28 and was raised.

The fact that no marked eggs disappeared from Nests 1 and 2 seems to show that the abnormally small thrush clutches were not the result of egg destruction by the Cowbirds.

Cowbird incubation and nestling periods.—Assuming a laying hour of about 5:00 a.m., which Hann (1941:211–212) found to be usual, the incubation period of the Cowbird egg in Nest 2 was about 11⅓ days, for it was

laid May 18, incubated at once, and hatched at 1:25 p.m. on May 29—that is, at that hour I found the nestling enclosed in just one half of its shell.

The nestling period of the Cowbird in Nest 3 was 12 days.

Wood Thrush feeds with female Cowbird.—The thrushes of a fourth nest did not seem to regard Cowbirds as enemies. During the building and laying periods at their nest a color-banded female Cowbird often fed in my banding trap just 20 yards southeast of their nest, and occasionally single males accompanied her and sometimes sang. The thrushes never showed concern; indeed, just two days before she laid her first egg the female thrush once fed in the trap along with the female Cowbird, while a male Cowbird stood just outside and the male thrush foraged a few yards away. Leaving the trap, these Cowbirds always flew in directions other than north; apparently the boundary of their range fell just short of including the thrushes' nest, and it was not parasitized.

Summary

Wood Thrush nest sites are chosen by the female; the male can influence her choice. Building is done by the female; rarely a male may work, but except during site selection none has certainly been seen to gather material. Height, placement, size and manner of building are described; like the American Robin, this species makes regular reversals of direction when molding. Nests are essentially complete after three days' work; slight touches are commonly given on two or three more days.

Sexual flights, other possibly stimulatory acts, and an attempt at copulation are described. One egg is laid daily, beginning one to three days after essential completion of the nest. Observed clutch size was 1 to 5, with 3 and 4 most common; clutches smaller than 3 all followed some disturbance of the breeding cycle. Laying is usually done between 9:00 a.m. and noon, but sometimes not until early afternoon; it is done earlier on cool than on warm days. Two broods are usual; second clutches were begun 9 to 12 days after first broods left the nest, but sooner when first nests were destroyed during incubation. Cowbird parasitism apparently inhibited Wood Thrush laying at all of three nests.

The brood patch develops within the week before laying starts. Incubation is by the female alone, beginning usually on the second laying day, and always before completion of the clutch; its gradual increase is described. Roosting on the nest begins with either the first or second egg. Some figures on amount and rhythm of incubation are given. Hatching most often occurs during daylight, and is spread over as much as 39 hours. The incubation period is about 12¾ days; an infertile egg was incubated 25 days; the female's incubating behavior is described. The incubation period of a Cowbird egg hatched by Wood Thrushes was about 11⅓ days.

One male learned of hatching by seeing the nestling and seeing his mate feed it, when it may have been but 17 minutes old; the male first fed it 17 minutes after that; it was fed three, probably five, times in its first hour. Feces are usually eaten, occasionally carried away. Brooding is by the female alone, throughout the nestling period of 12 to 14 days. The nestling period of a Cowbird raised by thrushes was 12 days. The thrushes do not seem to recognize the Cowbird as an enemy.

Both parents feed the fledglings, but not indiscriminately: the broods are divided between them, except that just before females resume laying they apparently stop feeding first broods. Several fledglings became partly independent at age 21 to 25 days, were last seen to be fed at 24 to 27, and were last seen at 21 to 27. Figures on nesting success are given. The male's activities during each phase of the breeding cycle are described. Song on the ground and in flight, and possible song by a female, are recorded.

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2620 Poplar Drive, Baltimore 7, Maryland, September 7, 1956

GENERAL NOTES

Marsh Hawk takes prey from Short-eared Owl.—While driving in the Buena Vista Marsh area near Bancroft, Wisconsin, on the afternoon of March 25, 1956, I saw an adult male Marsh Hawk (*Circus cyaneus*) diving repeatedly at a Short-eared Owl, (*Asio flammeus*) which was perched on the ground. After stopping the car I continued watching the episode with a seven power binocular at a distance of about 125 yards.

After a short time the owl flew up carrying what appeared to be a vole (*Microtus*). After a close chase lasting no more than 30 seconds the pursuing Marsh Hawk drove the owl upwards until at a height of about 150 feet the owl released its prey. The mouse fell to the road in front of me and was quickly seized and carried away by the hawk.—Daniel D. Berger, *Cedar Grove Ornithological Research Station, Cedar Grove, Wisconsin, May 10, 1957.*

Supernumerary rectrices in some raptors.—On January 8, 1956, while trapping and banding American Kestrels (*Falco sparverius*) in south Texas, we obtained a bird of this species near Encinal in Webb County which possessed 13 rectrices instead of the usual 12. The rectrix which appeared to be the supernumerary was about six millimeters shorter than the others and inserted between numbers 1 and 2 (numbered from the center outward) on the right side. All growth in this feather appeared to have terminated.

The bird was considered to be an immature male on the basis of the fault bars in the plumage—primarily in the remiges and rectrices. However, error in age determination by this method is possible. Of Parkes' (1955. *Wilson Bull.*, 67:194–199) aging criteria only the tail character, which is admittedly rather unreliable, would remain useful by early January, since the other characters would have been obliterated by the postjuvenal body molt. The tail character indicated that the bird was adult. On this particular bird we considered the fault bar aging method to be more reliable.

Dr. Erich Awender (personal correspondence, April 2, 1957) once took a nestling European Goshawk (*Accipiter gentilis*) that had a perfectly-developed extra tail feather which was inserted between numbers 4 and 5 on the left side. A similar occurrence was reported by Bakheet Talatashar (1951. *Falconer*, 2:59), a falconer, who trapped an adult Peregrine Falcon (*Falco peregrinus pelegrinoides*), presumably near his home in Khartoum, Egyptian Sudan, which had "thirteen tail feathers, all fully formed and feather-perfect."—Daniel D. Berger and Helmut C. Mueller, *Cedar Grove Ornithological Station, Cedar Grove, Wisconsin, May 10, 1957.*

Data on relative heart size of the Warbling Vireo and other passerines from high altitudes.—In an earlier account (1955. *Wilson Bull.*, 67:78–83) we offered some evidence in support of views held by Rensch and others to the effect that, in birds, the ratio of heart weight to body weight, or "heart ratio," increases with increase in altitude. The data included in that paper concerned only those species for which we had heart-ratio measurements from both high and low altitudes. Since relatively little has been published on heart size of birds from high altitudes (cf. Hartman, 1955. *Condor*, 57: 221–238 [esp. p. 226]), we are presenting data on heart ratios of 73 specimens of 24 species not included in our previous report. The specimens, obtained in the course of an expedition sponsored by the Museum of Vertebrate Zoology, were taken in the breeding season at elevations of 6700 to 12,000 feet in the White Mountains of extreme east-central California and adjacent Nevada. Subspecific status of the species in question may be

determined by consulting Grinnell and Miller (1944. *Pac. Coast Avif.* no. 27) and Miller and Russell's notes (1956. *Condor*, 58:75–77) on the distribution of certain forms in the White Mountains.

HEART RATIOS OF SOME PASSERINE BIRDS FROM THE WHITE MOUNTAINS OF CALIFORNIA AND NEVADA

	Males	Females
Sayornis saya. Say Phoebe.	1.04	
Contopus sordidulus. Western Wood Pewee.		1.37, 1.49
Eremophila alpestris. Horned Lark.	1.68 ± .08[1] (5)	
Parus gambeli. Mountain Chickadee.	1.43, 1.54, 1.67	1.34
Sitta carolinensis. White-breasted Nuthatch.	1.62 ± .06 (5)	1.46
Sitta canadensis. Red-breasted Nuthatch.		1.90
Thryomanes bewickii. Bewick Wren.	1.59	
Oreoscoptes montanus. Sage Thrasher.		1.37
Hylocichla guttata. Hermit Thrush.	1.55 ± .09 (4)	1.18
Polioptila caerulea. Blue-gray Gnatcatcher.		1.03, 1.58
Vireo gilvus. Warbling Vireo.	2.16 ± .14 (6)	
Vermivora virginiae. Virginia Warbler.	1.58, 1.59	
Dendroica petechia. Yellow Warbler.	1.55	1.38
Dendroica auduboni. Audubon Warbler.	1.41, 1.57, 1.73	1.37
Dendroica nigrescens. Black-throated Gray Warbler.		1.41
Oporornis tolmiei. Tolmie Warbler.	1.59 ± .06 (8)	
Molothrus ater. Brown-headed Cowbird.	1.52	
Piranga ludoviciana. Western Tanager.	1.27, 1.51	
Pheucticus melanocephalus. Black-headed Grosbeak.	0.96, 1.08, 1.29	
Passerina amoena. Lazuli Bunting.	1.38	1.34
Carpodacus cassinii. Cassin Finch.	1.39, 1.54, 1.55	
Loxia curvirostra. Red Crossbill.	1.74 ± .09 (6)	1.82, 1.98
Pooecetes gramineus. Vesper Sparrow.	1.24	1.14
Spizella breweri. Brewer Sparrow.	1.33	

[1]Standard error of the mean; parentheses enclose number in sample.

We should like to call particular attention to the extremely high heart ratio of the Warbling Vireo. In the six males the heart weight averages more than 2 per cent of the total body weight. An additional bird of undetermined sex had a ratio of 2.06. Of the seven June-collected specimens, three were from approximately 7400 feet elevation, three from 8200 feet, and one from 10,500 feet. It is possible that samples of males (whose ratios average larger than females) of certain other species taken at high altitudes would yield ratios comparable to those of the male vireos. An example is the Red-breasted Nuthatch (for which we have but one value). However, as far as present data indicate, the Warbling Vireo has a relatively heavier heart than any other passerine species. Indeed its heart ratio approaches that of the smaller species of hummingbirds (Hartman, 1954. *Auk*, 71:467–469), whose ratios are generally in excess of 2 per cent. At present we can offer no conjecture as to why the heart ratio of this vireo is so large in comparison with that of most other passerines.—FRANCIS S. L. WILLIAMSON, *Arctic Health Research Center, United States Public Health Service, Anchorage, Alaska, and* ROBERT A. NORRIS, *1918 Hahn Avenue, Aiken, South Carolina, July 5, 1957.*

Attraction of birds to salt licks placed for mammals.—On July 16, 1956, in a small meadow at 8000 feet elevation in Yosemite National Park, California, I flushed a group of about 20 Cassin's Finches (*Carpodacus cassinii*) from a block of salt that had been placed for the use of deer. I retired a short distance to watch the salt, and found that the Cassin's Finches alighted on and beside the salt cake and picked at it with their bills, removing and swallowing small pieces of salt. I suspended my mist nets near the salt, and on six days, July 16, July 18 to 22, captured and banded some of the birds that were attracted to the salt. Eight of the 642 Cassin's Finches banded had their legs and feet heavily parasitized by the scaly leg mite (*Cnemidocoptes mutans*), and the legs of 18 more were so swollen and encrusted that I could not band them. Two of the 32 Red Crossbills (*Loxia curvirostra*) banded were infested with this same parasite. I also captured two Evening Grosbeaks (*Hesperiphona vespertina*) and 71 Pine Siskins (*Spinus pinus*) at the salt block. No individuals of the last two species showed signs of mite infestations of the tarsi.—Don Bleitz, *Bleitz Wildlife Foundation, 1001 North McCadden Place, Los Angeles 38, California, November 7, 1956.*

Patterns in the use of left and right limbs in vertebrates.—Fisher's paper (1957) on the average preference of Domestic Pigeons (*Columba livia*) for landing on the right foot is especially interesting in demonstrating that the pattern is apparently not the same as in humans, and may vary with a number of factors. One would expect habit to determine one or the other usage in a set of actions, and thus avoid the necessity of choice. This one might expect to be more important in the more highly evolved animals. Since the small body of information that has been recorded about such patterns in vertebrates, other than man, is apparently little-known, the following notes that have come my way may be of interest.

Parrots tend to be left-footed in holding food (Friedmann and Davis, 1938); birds of prey tend to hold and carry food in the left foot (Lane); lions and tigers are either right- or left-pawed, and gorillas tend to be left-handed and with a more developed left arm (Lane, 1946); the rhesus monkey may be right- or left-handed and this is easily altered by training (Lashley, 1917).

Although elephants being right-tusked, mountain goats right- or left-hipped in sliding down mountains, Spanish fighting bulls having a master horn, and Texas longhorns a less-regular-shaped right horn (Lane, *op. cit.*), may not be quite the same type of phenomena, they are certainly collateral.

The asymmetrical condition in the skull of certain whales, notably sperm whales, is probably correlated with bone changes in phylogeny and not with behavior. But the crossing of the mandibles in crossbills (*Loxia*), the upper to the left predominating in the New World, crossing to the right in the Old World (Southern, 1957:125) seems to affect behavior in feeding—a "right-handed" bird holding the cone in one direction, a "left-handed" in the opposite way.

It has been held that puffins, which may carry up to 28 little fishes in their bills at one time, arrange the fish with the heads all to one side of the mouth, but this is erroneous, as they actually are held at random (Fisher and Lockley, 1954:287). Terns, however, are said to carry fish hanging down the left side of the bill (Fisher and Lockley, *loc. cit.*). Palmer (1941:98) has made an illuminating observation on this: a feeding flock of terns tends to rotate, birds diving from one side and then coming up and going to the other side of the flock. When a bird carrying a fish leaves the flock the fish always hangs down the same side of the bill. This is a natural result of the birds' swooping down from one side of the rotating flock only, while the school of fish is travelling in one direction.

Students interested further in the subject should consult Ludwig's 500 pages dealing with the question of left and right in both animals and plants, a volume not available to me.

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A. L. RAND, *Chicago Natural History Museum, Chicago 5, Illinois, July 29, 1957.*

Nesting of the Cattle Egret in the Virgin Islands.—The first specimen of the Cattle Egret (*Bubulcus ibis*) from the American Virgin Islands was taken on St. Croix on February 21, 1955 (Seaman, 1955. *Wilson Bull.*, 67:304–305). No evidence of breeding of this egret was found in 1955.

On May 29, 1956, while banding White-crowned Pigeons (*Columba leucocephala*) at Krause Lagoon, St. Croix, a small breeding colony of Little Blue Herons (*Florida caerulea*) and Snowy Egrets (*Leucophoyx thula*) was visited. Several Cattle Egrets were identified at this site immediately and their bright plumage, guttural cries and agitated behavior left no doubt that they were sharing the mangroves (*Rhizophora mangle*) with their companion herons in breeding activities. There were about 30 breeding herons on this mangrove island on this date. All young were about two weeks old, and mixed up helter-skelter through their many-limbed home. Although I felt very sure that some of the young observed belonged to the newly-arrived Cattle Egrets, no report was made, since none of the nests or eggs found was identified positively.

On February 26, 1957, 10 Cattle Egrets were observed at the heronry at Krause Lagoon. There were no nests on this date but breeding behavior was evident. On April 23, three nests containing two pale, blue-green eggs each were identified at the old site. They were typical heron nests, loosely constructed of twigs and placed on the western or lee side of the mangrove clump or "island."

On April 30, four nests of the Cattle Egret were found; these contained 2, 2, 1, and 3 eggs, respectively. Hatching was in progress in one nest on this date, and it was completed in three by May 7. On the latter date the bills of the nestlings that had

hatched on April 30 were noticeably short and stout (see photograph). On May 14, it was discovered that all eight eggs in the four nests had hatched.

It is interesting to note the social habits of the three species on this small mangrove "island" which had been utilized for nesting by the Little Blue Herons and Snowy Egrets for many years. The Little Blue Herons took up quarters by themselves on the east or windward side of the mangrove clump, whereas the Snowy and Cattle egrets nested on

the lee side of the island. When danger threatened, all the young climbed together to the center of the tree. Later, as the parents returnd to look at their young or bring food, each group found its own nest and parents. The Cattle Egrets were apparently accepted in this old community with no undue animosity or discrimination. No other breeding site of this heron has been located on the island.—G. A. SEAMAN, *Box 474, Christiansted, St. Croix, Virgin Islands, August 20, 1957.*

Nesting habitat of the Black-bellied Tree Duck in Texas.—On a recent trip to the Lower Rio Grande Valley of Texas, the writers were shown 10 nests of the Black-bellied Tree Duck (*Dendrocygna autumnalis*), by Mr. R. J. Montgomery, near Rio Hondo, Cameron County. All of the nests were located in hollow trees near a small lake; eight were in ebony (*Pithecolobium flexicaule*) trees, and two were in hackberry (*Celtis laevigata*). Nesting cavities were located in the main trunk, and the entrance hole was seldom over three or four feet from the ground.

Although there had been much clearing of accompanying vegetation, in most cases the

favored habitat appeared to be a thicket composed of characteristic trees and shrubs of this semi-arid region. Nest trees were along the border or in openings in the thicket. Dominant plants in such thickets were ebony, mesquite (*Prosopis chilensis*), retama (*Parkinsonia aculeata*), huisache (*Acacia farnesiana*) and several species of cactus (*Opuntia* spp.).

Other birds nesting in this habitat included the Red-billed Pigeon (*Columba flavirostris*), Mourning Dove (*Zenaidura macroura*), White-winged Dove (*Zenaida asiatica*), Ground Dove (*Columbigallina passerina*), Inca Dove (*Scardafella inca*), Scissor-tailed Flycatcher (*Muscivora forficata*), Kiskadee Flycatcher (*Pitangus sulphuratus*), Curve-billed Thrasher (*Toxostoma curvirostre*), and Boat-tailed Grackle (*Cassidix mexicanus*).

The writers are grateful to Mr. Montgomery for showing them the tree-duck nests on his lands.—Brooke Meanley and Ann Gilkeson Meanley, *P. O. Box 1365, Alexandria, Louisiana, August 1, 1957.*

Interspecific defense of roost site by Loggerhead Shrike.—In late November, 1956, a Loggerhead Shrike (*Lanius ludovicianus*) established a feeding territory in the vicinity of my home at the northwest edge of Midland, Texas. Within this territory, he chose an evergreen sumac (*Rhus virens*) about 12 feet in height as his nightly roosting place. He seldom sat in this bush during the day. Three days after the shrike began roosting in the sumac bush, a Pyrrhuloxia (*Pyrrhuloxia sinuata*) entered the bush in the afternoon. The shrike was then sitting on a wire about 150 feet from the bush. He immediately flew to the bush and alighted on one of the topmost limbs, uttering harsh, scolding cries. The Pyrrhuloxia left precipitously. The same thing occurred at various

times of day, for three successive days, until the Pyrrhuloxia no longer came to the shrike's roosting "tree."

A week later, a Cactus Wren (*Campylorhynchus brunneicapillus*) entered the sumac bush about noon. He "sang" there several minutes before the shrike dived, squawking, into the bush. The Cactus Wren moved to the other side of the bush and scolded the shrike. The shrike then flew directly at the wren, but the latter flew to a near-by tree, still scolding. After the wren left the sumac, the shrike showed no more interest in the wren. Similar occurrences took place for five consecutive days, after which the Cactus Wren began singing from a tree outside the shrike's feeding territory.

Another Loggerhead Shrike had a feeding territory about 750 feet south of the roost tree, but never attempted to alight in the bush.

Although the shrike took up residence in the area in early September, he did not begin defending the sumac until frosts had hastened the loss of leaves from other trees and shrubs in the vicinity.

The incidents reported above are of interest because no mention is made in the literature of such defense of roosting trees by shrikes. Alden H. Miller (1931. *Univ. Calif. Publ. Zool.*, 38(2):148) emphasizes that Loggerhead Shrikes defend their winter feeding territories against other shrikes. He also mentions (p. 158) that shrikes have within their breeding territory a favorite roosting place, but does not state whether he observed such roosting places in the winter territory, or whether such roost-trees are defended. K. E. L. Simmons (1951. *Ibis*, 93:409–410) cites instances of competition for feeding territory between two species of shrikes (*Lanius collurio* and *L. nubicus*) in Egypt, but does not mention defense of the roost tree.—Frances M. Williams, *Rt. 2, Box 45-B, Midland, Texas, August 9, 1957.*

Blue Jay feeding on a dead fledgling House Sparrow.—On May 25, 1957, a Blue Jay (*Cyanocitta cristata*) was noted pecking repeatedly at a dead bird on a macadamized road at the Agricultural Research Center, U. S. Department of Agriculture, Beltsville, Prince George's County, Maryland. It reared back again and again as it pulled vigorously on a slender piece of intestine that would not yield. When I approached, the jay flew to perch in a tree near by, deserting its prey which proved to be a young House Sparrow (*Passer domesticus*).

An examination of the sparrow, which was still warm, showed that the skin was torn from the back of the head where a hard blow apparently had been struck. The entire right side of the bird's body, including its ribs, the right side of the sternum, and the scapula was gone. The muscled portion of the right wing was completely skinned, and the humerus was broken into two pieces. The upper part of the right rear leg was skinned also. The body cavity was stripped of all organs except the kidneys. A piece of the trachea remained. A short piece of intestine was lying on the road near the sparrow.

The sparrow had a thick yellow rictal band. Wing and tail feathers had emerged from their sheaths; the longest feathers measured 36 and 22 mm. respectively, including the sheaths.

Victor P. Chase (1899. *Wilson Bull.*, 11:57) describes a Blue Jay attacking and killing a "a newly fledged bird" of a group of House Sparrows that were fluttering about it as it ate cherries from a tree. The jay became frightened and left its prey. Hiram M. Stanley (1898. *Science*, New Ser., 8[190]:223) records a Blue Jay seizing and eating one of four fledglings from a House Sparrow nest which had been destroyed.—Donald H. Lamore, *2C, Gardenway, Greenbelt, Maryland, September 3, 1957.*

Nesting of the Chimney Swift in Colorado.—The only published record of the occurrence of the Chimney Swift (*Chaetura pelagica*) in Colorado is an account by Thompson G. Marsh (1931. *Auk*, 48:427–428) who observed one individual over the duck pond in Denver's City Park on May 16, 1930. For the last five years the species has appeared each spring at the town of Boulder, which lies at the base of the foothills of the Rockies and which is about as far west as the swifts could be expected to penetrate the high plains of central Colorado. They remained to breed during the summers of 1956 and 1957.

On May 11, 1953, a familiar twittering over the downtown section of Boulder led me to glance upward and I observed four Chimney Swifts above the buildings. The birds were also observed later in the day by Gordon Alexander and by Douglas Alexander. A late spring cold front came through the region the same evening, bringing freezing temperatures and low clouds which inactivated all airborne insects for several days. The swifts were not seen again that year and it is possible that they perished.

The following year, three swifts appeared in Boulder again on May 14, but did not remain. In 1955, two birds were seen over Boulder on May 22, but did not remain, and as in the previous year were not seen again for the rest of the summer.

On June 1, 1956, Douglas Alexander and I saw two swifts joined by a third which was emerging from a chimney of a building in downtown Boulder. As we watched they made repeated passes over the chimney but did not enter it again. A vigil of several days at this location proved fruitless and it was thought at first that the birds had left the region. However, on June 8, three birds were seen circling a building at the south edge of the University campus and four were seen in this vicinity on several subsequent dates in June. On July 6 I devoted the entire day to observing the circling, feeding, and flight directions of the swifts. The nest of one pair was located the following day in the south chimney of the Chi Omega sorority house at the edge of the University campus. I spent several hours on July 8 in the company of L. M. Baylor watching the swifts enter and leave the chimney, and later in the week I observed a young swift exercising its wings while clinging to the top of the chimney.

On July 13, six birds were observed flying around Old Main in the center of the campus and on the 14th, by climbing to the top of the building, I found a second nest in one of the many chimneys. It was approximately three feet below the top of the chimney and contained four nearly-fledged young. During the last week in July, 10 swifts were seen circling the campus every day. Six of them appeared to have a much more diaphanous plumage than the other four, permitting the light to pass through more readily.

In the summer of 1957, five swifts appeared in Boulder again during the last week in May and on June 2 a pair reoccupied the Chi Omega nesting site. During the rest of June as many as six were seen at different times over various parts of Boulder but no effort was made to locate the other nesting sites.—Owen A. Knorr, *Department of Biology, University of Colorado, Boulder, Colorado, November 22, 1957.*

ORNITHOLOGICAL NEWS

Members should be completing their plans to attend the Thirty-ninth Annual Meeting at Wheeling, West Virginia, April 24–27. A variety of field excursions are planned for visitors to that ornithologically interesting region.

We are indebted to Don R. Eckelberry for making available the painting of the Violet-headed Hummingbird from which the frontispiece was printed.

We welcome the addition of Andrew J. Berger of the University of Michigan and Robert A. Norris of the University of Georgia to the Editorial Advisory Board of *The Wilson Bulletin*. Both began serving in this capacity in the latter part of 1957.

Ornithologists planning to attend the Twelfth International Ornithological Congress at Helsinki, June 5–12, may be interested in the possibility of travelling by surface vessel leaving New York on May 24. Further details may be obtained by writing

Mrs. Doris Huestis Speirs,
Cobble Hill, R.R. No. 2
Pickering, Ontario.

A symposium, "Concepts in Biology," appearing in the April, 1958, issue of *Behavioral Science*, may be of interest to ornithologists and teachers of biology. Contributors include Ernst Caspari, Ernst Mayr, George G. Simpson and Sewall Wright. Single copies may be obtained from the Mental Health Research Institute, University of Michigan, Ann Arbor, for $1.75.

The Division of Biological and Medical Sciences of the National Science Foundation announces that the next closing date for receipt of basic research proposals in the life sciences is May 15, 1958. Disposition of the proposals will be made approximately four months after the closing date. Inquiries should be addressed to the National Science Foundation, Washington 25, D.C.

ORNITHOLOGICAL LITERATURE

THE WARBLERS OF AMERICA. By Ludlow Griscom, Alexander Sprunt, Jr., and many other contributors. Devin-Adair Co., New York, 1957: 8 × 10 in., xii + 356 pp., 33 color plates, 3 figs., 51 range maps and many black and white drawings by John Henry Dick. $15.00.

This work evolved from the gradual fulfillment of the artist's desire to paint all the warblers of the United States and Canada. The senior authors, Griscom and Sprunt, agreed to prepare or accumulate the accompanying text. As the project neared completion, it was decided to portray also those species which occur in Mexico, the West Indies, and Central and South America, thus including in one volume every species of the Parulidae. This was a fortunate decision, indeed, for the text embracing the North American species adds little to the published knowledge and would not justify another expensive bird book. The informative chapters on and the plates of the neotropical species, however, are definite contributions to American ornithology. The extension of scope resulted in a change of title from "The Warblers of North America" to the present name, a change that will be welcomed by all who are familiar with Chapman's "Warblers of North America" and resent the all too frequent use of the original titles of classic works for new books published by different authors years later. The title on the jacket, unfortunately, was not changed.

A publisher's preface is followed by "An Introduction to the Warbler Family," reprinted from Alexander Skutch's "Life Histories of Central American Birds" (*Pacific Coast Avif. No.* 31, 1954). There are chapters by Griscom on classification, the techniques of warbler study, songs, and geographical distribution. One by W. W. H. Gunn and Donald J. Borror analyzes the songs of 39 North American species. A final introductory chapter is a tabular comparison of warbler foraging ranges.

The bulk of the book comprises the individual write-ups for the warblers breeding in the United States. The hybrid Brewster's and Lawrence's are included in the 60, and Sutton's is here considered a breeding warbler. Sprunt has written 31 accounts, and the balance has been contributed by various experts familiar with the subject species. That more of them were not so assigned to experts familiar with a species on its breeding ground is a major shortcoming of the book. Descriptions are limited to field characteristics. In conformity with the A. O. U. Check-list, subspecies are "generally suppressed," but the old subspecific common names are listed as "local names." If such names are to be used, would it not be better to call them "regional names" and limit the term local to names which have always been considered local, such as Golden Swamp Warbler, Summer Yellow Bird or Yellow-rump?

Seven excellent chapters briefly described the resident and migrant warblers of Mexico (by Emmet Reid Blake), the West Indies (James Bond), Central America (Skutch), Panama (Eugene Eisenmann), and South America (Blake). The behavior of the family north of the United States is ably discussed in chapters on Alaska (Frederick C. Lincoln), British Columbia (J. A. Munro), the Prairie Provinces (W. Earl Godfrey) and Eastern Canada (Roland C. Clement and Gunn).

There is a biographical sketch of each contributor. Appendix A is a classification of the Parulidae, but no author is credited with the compilation. Appendix B is a suggested reclassification by Griscom. I find it confusing to find him lumping *Myiothlypis*, *Idiotes* and *Phaeothlypis* into *Basileuterus*, yet do not find these three discarded genera in the supposedly present classification of Appendix A. Appendix C, "The Gulf Migration

Routes of 38 Eastern Warblers," is an excerpt from Henry M. Stevenson's migration paper in the March, 1957, *Wilson Bulletin*.

Two chapters conclude with short bibliographies, and it is regrettable that this is the extent of the practice, particularly inasmuch as the text contains innumerable references to other authors by name and with date of publication. There is an index.

The plates are generally attractive, and the artist has made his warblers lifelike in proportions and actions. His choices of backgrounds are pleasing, and the North American species are usually depicted with not more than one or two species to a plate. Most warblers seem to be about three-quarters natural size, but the caption pages do not give any scale. Scientific names are lacking on the caption pages for the North American species but are present for the neotropical. A lack of liaison between text and plate is apparent when we read (p. 186) that the name, Palm Warbler, is a misnomer and then find (Plate 22) the individuals of that species superimposed upon the fronds of a palm.

The six-color offset process leaves much to be desired. Many plates appear to reproduce in paler tones than normal. Reproduction varies from copy to copy. I know of one volume in which the Blackburnian Warbler is hopelessly off color. In mine it is excellent. My Worm-eating Warbler (Plate 2) and Northern Waterthrush (Plate 23) have green backs which in no manner approximate the true colors of these species. The immature Black-throated Green Warbler (Plate 18) has a chestnut stripe on crown and back, and the male Yellowthroat (Plate 25) also has a chestnut crown which, while probably intended simply as highlights, have reproduced poorly. The male Prairie Warbler (Plate 21) is badly out of register in my copy. The publisher's comment (p. x) that Chapman's work has "inferior plates" will not sit well with those of us who are admirers of the artistry of Louis Agassiz Fuertes, including even his earlier works. Small in size, perhaps, but not inferior.

Careful editing would have called for a more standardized form in the individual accounts and the summaries which conclude them. Many write-ups give valuable descriptions of nesting habitat and breeding behavior. Some describe but a single type of habitat. Others ignore breeding altogether and are devoted to observations during migration. Egg measurements are given in only four summaries. Length of bird is omitted in one. Material is repeated in the summaries which also appear in the narrative. The useful breeding range maps do not always agree with the ranges given in the text. The map for the Black-throated Blue (p. 123) indicates that Cairn's Warbler breeds north to New York State; that for the Myrtle (p. 126) does not indicate that Myrtles breed south into Pennsylvania; that for the Louisiana Waterthrush (p. 199) does not recognize that this species breeds abundantly in Delaware and on the Eastern Shore of Maryland.

Careful editing would have prevented, too, the discrepancy between Griscom's statement (p. 20) that the Blackpoll can sing at a frequency of 14,000 vibrations and Sprunt's use (p. 172) of the figure 10,225. Careful editing and proof-reading would have caught many of the errors of punctuation and such unnecessary mistakes as the use of the date 1955 on page 15, when the correct date is obviously 1957, and the inexcusable line transposition in the Eisenmann biographical sketch on page 340.

Its sub-title calls this "A Popular Account of the Wood Warblers." Instead, the final result is a hybrid between popular and technical. Griscom's proposed reclassification does not belong in a popular book. The account of John Bachman does not belong in either a popular or technical bird book when, according to the publisher, "our biggest task has been to keep the number of pages down to reasonable length." I would hazard the guess that the "meat" in this volume could have been condensed into one-quarter less page space than was used, and the space thus freed could have been utilized to excellent

advantage by adding information which would have made this a more truly definitive work. One of the reasons given for this publication (p. x) is that Bent's "Life Histories" is out of print. Yet (p. xi) we are told to consult Bent when further data are required! There would be less need to consult Bent (and Chapman) if the space in this volume had been used more judiciously.

In striving to be both popular and technical, the books falls short of its true potential in either category. If I seem unduly critical, it is because I thought this long-awaited book would be the new definitive warbler work. Instead, it has its place along with Chapman and Bent in my library and contributes much which they do not offer, but it does not supercede them.—PHILLIPS B. STREET.

VERTEBRATES OF THE UNITED STATES. By W. Frank Blair, Albert P. Blair, Pierce Brodkorb, Fred R. Cagle, and George A. Moore. McGraw-Hill Book Company, New York, 1957: 6¾ × 9½ in., ix + 819 pp., illus. $12.00.

This important book is intended to replace the old familiar manuals of Pratt and Jordan as a basic text and reference "for courses in vertebrate classification, ecology, and natural history." This aim has been kept in mind when studying the book preparatory to review.

Since the names of the authors as listed above are in a different sequence from their contributions, it may be noted here that Frank Blair wrote the introduction and the section on mammals, Moore the fishes, Albert Blair the amphibians, Cagle the reptiles, and Brodkorb the birds. The introduction is a brief but well-written survey of the history, characters, classification, nomenclature, and North American distribution of the vertebrates. In the latter connection, I feel that it would have added much in value and relatively little in bulk (and gained additional purchasers for the book) had the northern limit not been set at the artificial border between Canada and the United States. I find that widening the scope of the book to include Canada and Alaska would have necessitated the addition of only 29 species of birds, less than 40 of mammals (authors disagree on species limits here), and *no* species of reptile or amphibian; I made no attempt to count the fishes.

By far the most valuable single contribution of the book to the current literature of the vertebrates is the section on fresh-water fishes by Moore. Keys and descriptions of the other groups are widely available, but Moore's chapter represents the only complete and up-to-date reference for the fishes. The phrase "up-to-date" is used advisedly; for example, *Notropis callitaenia* Bailey and Gibbs is in its proper place in the text although described as late as August, 1956.

Since *The Wilson Bulletin* is an ornithological journal, only the chapter on birds by Pierce Brodkorb will be reviewed in detail here. This is the only chapter of the book lacking a bibliography, but I have learned that one was prepared and somehow omitted during the course of printing. This unfortunate accident will undoubtedly be rectified in any future edition.

Perhaps it is because I am an ornithologist and can thus read the bird chapter more critically than I can the others, but I feel that the quality of this section is not up to the standard set by the rest of the book. Certainly the illustrations are inferior; they are fewer (key characters in the other groups are excellently illustrated) and in many cases are downright crude, contrasting strongly with those of the other chapters. The introductory section dealing with birds in general seems too brief, and is heavily weighted in favor of those aspects of anatomy which apparently interest Dr. Brodkorb most. Thus, of a total of nine introductory pages (⅓ illustration, ⅔ text), more than two full pages

are devoted to the classification of the loops of the small intestine, while the taxonomically important anatomy of the syrinx and its muscles is disposed of in four lines. A serious omission from the student's viewpoint is any discussion or illustration of the external features of a bird or the nomenclature of the wing feathers.

The most serious shortcoming of Brodkorb's work, and one which so irritated this reviewer as to blind him temporarily to the good features, is in the handling of classification and nomenclature. This purports to be that of the fourth edition of the American Ornithologists' Union Check-list, with supplements through 1956 (the last supplement issued). According to Brodkorb, "in the few cases in which the nomenclature of the manual differs, the A.O.U. name is supplied in a footnote." I have found no less than three regroupings at the family level, 11 changes at the generic level, 12 changes at the specific level, and a number of rearrangements of genera within a family. And I undoubtdly missed some. The question is *not* whether I, as a taxonomist, agree with the changes from A.O.U. usage introduced by Brodkorb. Some of these are widely accepted elsewhere; others appear to be first introduced into the literature here. On these matters, more later. But it cannot be emphasized too strongly that a college text is *not* the place to indulge in taxonomic innovations. Most of the intended users of this book will expect to be able to correlate this chapter with other bird literature in their possession, and will not be taxonomic ornithologists. It is unfair and confusing to these students to depart from what is generally regarded as the standard classification of North American birds. Even in those cases in which Brodkorb has added an explanatory footnote (and this was *not* done in every case of departure from A.O.U. nomenclature), space does not permit him to present anything like an adequate justification of the change from the viewpoint of the taxonomist. If Dr. Brodkorb feels strongly about some of these taxonomic matters (and his wording in several cases suggests that he does), he should have published papers presenting his views in accepted taxonomic fashion. As it is, he has imposed his own ideas (some of which will find little acceptance among taxonomists) upon a captive audience, few of whom will be competent to judge for themselves the merit of the changes.

As it is, Brodkorb has been quite inconsistent in his selection of changes (predominantly "lumpings"). At the generic level, for instance, he suppresses several widely-accepted genera but continues to maintain *Mareca*, *Spatula*, *Rhynchophanes*, *Chlorura*, etc. Some of the taxonomic changes suggested, and some of the diagnoses of families and genera, give evidence of a lack of familiarity on the part of the author with the birds of the rest of the world. Brodkorb states that the monotypic genus *Leucophoyx* cannot be maintained for the Snowy Egret, but merges it with *Florida* without a word to indicate how he believes *Egretta*, *Mesophoyx* or *Demigretta* fit in. The genus *Baeolophus* is unaccountably revived for the four A.O.U. species (reduced to three by Brodkorb, following Dixon) of crested titmice, with a generic diagnosis completely meaningless if the titmice of the world are considered. The "differences" cited between *Chamaea* and the "Timeliidae" [*sic*] do not hold; Brodkorb could not have compared *Chamaea* with *Chrysomma*. The swallow genera *Hirundo* and *Petrochelidon*, linked by intermediate Old World species and thus lumped by many authors, have been placed at opposite ends of the family by Brodkorb.

There are numerous errors of fact of various degrees of importance. The Northwestern Crow, stated by Brodkorb to be "*Corvus brachyrhynchos caurinus* Baird of A.O.U.," was raised to specific status in the 1945 Check-list supplement. All parrots are not hatched naked. The Poor-will is not the only goatsucker that lays unspotted eggs; the western race of Whip-poor-will sometimes does so. The nuptial plumage of the male Bobolink is acquired by a complete prenuptial molt, *not* by wearing off the tips of the female-like

winter plumage. The key to genera of Corvidae includes both *Xanthoura* and *Cyanocorax*, although both names apply to but a single U. S. species, the Green Jay.

As for the keys themselves, only actual use by students will determine their value. Making such keys is a difficult and thankless task, and Brodkorb has done, by and large, an excellent job in making his keys valid for birds in any adult plumage stage by concentrating on structural characters. This can be overdone, however, as in separating the two North American pipits by a hind toe and claw/tarsus ratio rather than by the immediately obvious difference in streaking on the crown (which is not even mentioned in the text). A number of Brodkorb's keys, in fact, remind me of the old story of the "two little morons" who worried for days about how to tell their respective horses apart, until they finally discovered that Blackie was an inch taller than Whitey!

Having had experience with steering students through ornithological keys, I noted a few characters which I can confidently predict as troublemakers. In the key to orders, the Psittaciformes are defined as possessing a cere, and so they do. But in the two North American species the cere is feathered, and it will be difficult to demonstrate to students that these parrots have "a membranous swollen covering of the base of the upper bill, through which the nostrils open" (glossary definition). In the key to families of the Charadriiformes, the student is asked whether his specimen has the anterior toes "fully webbed" or "with only basal webs or none." I sympathize with the instructor who must explain to a student why the Black Tern belongs with the former and the Avocet with the latter.

Brodkorb is guilty of occasional irritatingly authoritarian pronouncements. On p. 520, for instance; "To make the divisions of the Passeriformes the equivalent of the divisions in other orders, it would be necessary to reduce the 4 commonly recognized suborders to family status." This is an unwarranted exaggeration. Granted that several currently recognized families of Passeriformes are poorly defined and merge into one another, there are others which are decidedly more distinctive than some families recognized by most authorities (including Brodkorb) within such orders as Procellariiformes, Galliformes, and Charadriiformes.

A few errors of omission have been noted. The Spotted-breasted Oriole, European Goldfinch, and the eastern introduced colony of House Finch are not mentioned, although their status in our avifauna is similar to that of the two *Streptopelia* doves, which are included in the book. Some plumages are omitted; eclipse plumages of the ducks and winter plumages of some of the warblers, for example. The Dusky and Cape Sable Seaside sparrows, carried as full species in the A.O.U. Check-list, are not mentioned at all. Presumably Brodkorb lumps these with *Ammospiza maritima*, but the description for the latter would certainly puzzle a student with a specimen of *A. nigrescens* in hand.

Unquestionably the most valuable contribution Brodkorb has made is the series of modern summaries of the characters, particularly anatomical, of the orders and families. Minor faults can be found with some of the non-anatomical generalizations, but a real service has been done for students of ornithology by assembling this material in such covenient form. Many of the generic diagnoses are equally valuable, but suffer to some extent because of controversies as to generic scope in some groups. And occasionally the generic diagnoses depend too much on one another, resulting in chains of "Like —, but . . ." See especially the family Icteridae in this regard.

The book as a whole has a combined glossary at the end; this may be a slight inconvenience, but has probably saved space by avoiding duplication of definition which would occur with sectional glossaries. A spotcheck showed a few ornithological terms which should probably have been included in the glossary, but in general it appears quite thorough.

In summary, then, the book as a whole will undoubtedly prove to be an exceedingly useful text for students, and reference for vertebrate zoologists in general. The section on birds has some decided faults and weaknesses, and should be rather thoroughly revised for any future edition, but it contains much valuable material not readily available elsewhere.—KENNETH C. PARKES.

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